THE PHYLOGENETIC RELATIONSHIPS OF SOFT-SHELLED TURTLES (FAMILY TRIONYCHIDAE)

PETER ANDRE MEYLAN

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 186 : ARTICLE 1 NEW YORK : 1987

Recent issues of the *Bulletin* may be purchased from the Museum. Lists of back issues of the *Bulletin, Novitates,* and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, New York 10024.

THE PHYLOGENETIC RELATIONSHIPS OF SOFT-SHELLED TURTLES (FAMILY TRIONYCHIDAE)

PETER ANDRE MEYLAN
Thorne Fellow
Department of Vertebrate Paleontology
American Museum of Natural History

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Volume 186, article 1, pages 1–101, figures 1–34, tables 1–22
Issued June 26, 1987
Price: $9.00 a copy

ISSN 0003-0090

CONTENTS

ABSTRACT

Phylogenetic analysis of 113 characters of the osteology of the 22 living species of trionychid turtles and representatives of all other living turtle families, provides abundant evidence on the relationships of soft-shelled turtles to other turtles and on the interrelationships within the family. These data suggest that the family Trionychidae shares a unique common ancestor with the Dermatemydidae, Kinosternidae, and Carettochelyidae, and that the Kinosternidae share a unique common ancestor with the Trionychidae and Carettochelyidae. Furthermore, it appears that the staurotypine kinosternids are most closely related to the Trionychidae and Carettochelyidae. Carettochelyids and trionychids share numerous unique features and clearly constitute a monophyletic group.

Within the Trionychidae, the subfamilies Cyclanorbinae and Trionychinae are recognized as monophyletic clades. Recognition of three cyclanorbine genera, *Cycloderma, Cyclanorbis,* and *Lissemys,* is warranted. Within the Trionychinae, four distinct clades are recognized. The *Trionyx cartilagineus* group includes *Chitra indica* and *Pelochelys bibroni,* on the basis of the unique location of the foramen posterior canalis carotici interni, and features of the trigeminal region. The North American group includes *T. triunguis, T. euphraticus, T. swinhoei, T. ferox, T. spiniferus,* and *T. muticus,* and can be recognized by the presence of eight or fewer neurals (first and second are fused), deeply emarginate prefrontals, and a large contribution by the parietal to the processus trochlearis oticum. The Indian group includes four species: *T. gangeticus, T. hurum, T. leithii,* and *T. nigricans*; all exhibit a free first neural, five plastral callosities, and intermediately extended epiplastra. Lastly, the *T. steindachneri* group, which includes *T. steindachneri, T. sinensis,* and *T. subplanus,* is diagnosed by a descending spine of the opisthotic that divides the fenestra postotica in most specimens.

Two equally parsimonious arrangements of the Trionychinae differ in the placement of the North American clade. In one, this clade is the sister group of the *T. cartilagineus* clade; in the other, it is the sister group of the *T. steindachneri* clade. In both, the Indian group is paraphyletic and gives rise to the *T. steindachneri* clade.

A revised classification of the family Trionychidae is provided. The use of 2 subfamilies, 6 tribes, and 14 genera is recommended. This expanded taxonomy will more completely reflect the hierarchical relationships that reflect recency of common ancestry as determined by the cladistic analyses.

INTRODUCTION

Within recent years a fundamental revision of the systematic relationships of turtles has begun. This revision was precipitated by Gaffney (1975), who presented a reorganization of the Testudines using the cladistic method (as outlined in Gaffney, 1979a; Wiley, 1981). Other authors have followed Gaffney's lead in applying this method to problems in chelonian systematics, resulting in a much clearer understanding of the phylogenetic relationships among turtle taxa. Concise hypotheses of the relationships within most families are now available (Proganochelyidae, Gaffney and Meeker, 1983; Chelidae, Gaffney, 1977; Baenidae, Gaffney, 1972; Meiolaniidae, Gaffney, 1983; Chelonioidea, Gaffney, 1976; Kinosternidae, Hutchison and Bramble, 1981; Trionychidae [shell only], Meylan, 1985; Emydidae, Hirayama, 1985; Testudinidae, Crumly, 1982, 1985) and are summarized by Gaffney (1984). The largest remaining family for which a complete cladistic study does not exist is that comprising the soft-shelled turtles, the Trionychidae.

This gap is significant, considering the large size, abundance, and great age of the family. The Trionychidae includes more than 250 named species (ca. 230 fossil and 22 extant) and occurs on every continent except Antarctica. It is a very old family, with definite representatives from the Cretaceous (Romer, 1956). Representation of this family in the fossil record is considerable, although difficult to document because few authors treat the fossils of this troublesome group. The best evidence of its ubiquity is reported by Hutchison (1982), who showed that the Trionychidae has the most continuous record of 11 reptile families examined from the Cenozoic of western North America.

Although authors do not agree on the relationships of trionychids to other turtles, I have never seen a single reference doubting the monophyly of the family. It is so distinctive that some authors have placed the family in a separate suborder equivalent to the Cryptodira and Pleurodira (Boulenger, 1889; Siebenrock, 1909; Bergounioux, 1932, 1955), an arrangement for which Loveridge and Williams (1957) found some support. Modern morphologists argue that this family is a group of aberrant cryptodires allied to the Carettochelyidae, Dermatemydidae, and Kinosternidae (McDowell, 1961; Albrecht, 1967; Zug, 1971; Gaffney, 1975, 1984). But others disagree, arguing that on the basis of karyology the Trionychidae, along with the Carettochelyidae, is the sister group of all other cryptodires (Bickham et al., 1983). On the basis of serological tests, Frair (1983) supported the placement of the family in its own suborder.

Among those workers willing to place the Trionychidae among the Cryptodira, there is difference of opinion as to which cryptodire families are the closest relatives of soft-shelled turtles. Since its discovery, *Carettochelys* Ramsay (1886) has been considered closely related to the Trionychidae, although some authors were confused by false reports of mesoplastra in this genus (Boulenger, 1889; Pritchard, 1967). Among the authors who have recognized close relationship between *Carettochelys* and the Trionychidae (Boulenger, 1889; Baur, 1890, 1891b; Waite, 1905; Siebenrock, 1902, 1913), some have recommended that superfamilial status be recognized (Trionychia, Hummel, 1929; Trionychoidea, Walther, 1922).

Several morphologists (Baur, 1891a; McDowell, 1961; Albrecht, 1967; Zug, 1971; and Gaffney, 1975, 1984) have allied the Trionychidae and Carettochelyidae with the Dermatemydidae and the Kinosternidae. Gaffney (1975) applied the name Trionychoidea to this group. This enlarged concept of the Trionychoidea is in clear conflict with the frequent association of the Kinosternidae with the Chelydridae and the inclusion of these two families in a clade with the Emydidae and Testudinidae. This latter arrangement was proposed by Williams (1950) and is based on the morphology of the cervical vertebrae and other osteological characters and has been followed by Romer (1956), Pritchard (1967, 1979a, 1979b), Mlynarski (1976), and others. Karyotypic data have recently been cited which partially support this arrangement (Bickham and Carr, 1983). It is obvious from these various arguments that the phylogenetic position of the family Trionychidae within the Testudines is still in question.

A narrower but equally urgent problem concerns the interrelationships within the family Trionychidae. The lack of resolution of relationships within the family is indicated by the current placement of nearly all species (ca. 235) in a single "wastebasket" genus, *Trionyx*. For more than 50 years since the major revision by Hummel (1929), there has been a strong tendency to synonymize trionychine genera (except *Chitra* and *Pelochelys*) with *Trionyx* (Bergounioux, 1955; Romer, 1956; Huene, 1956), with the result that 47 generic names are now considered synonyms (Smith and Smith, 1980). The apparent reason for this is not uniformity of morphology, but rather an absence of a complete and systematic interpretation of the characters. The large number of taxa and high intraspecific variability in the shape and degree of ossification of both the shell and skull make any study of trionychid relationships using a phenetic method extremely difficult. The most important recent studies are those of Loveridge and Williams (1957) and De Broin (1977). On the basis of osteological characters, color pattern, and geography, Loveridge and Williams arrived at the arrangement redrawn as figure 1. The De Broin (1977) arrangement is based largely on characters of the shell and skull (especially the palate), but is given in insufficient detail to allow construction of a branching diagram. Both the Loveridge and Williams (1957) and De Broin (1977) arrangements contain features which appear in a cladistic analysis of the family based on shell morphology (Meylan, 1985).

Phylogenetic analysis provides a methodological breakthrough that has allowed elucidation of trionychid relationships. This method results in arrangements of taxa in hierarchies of internested natural groups. Because uniquely derived character states are used only from that point in the hierarchy beyond which they are shared by all taxa,

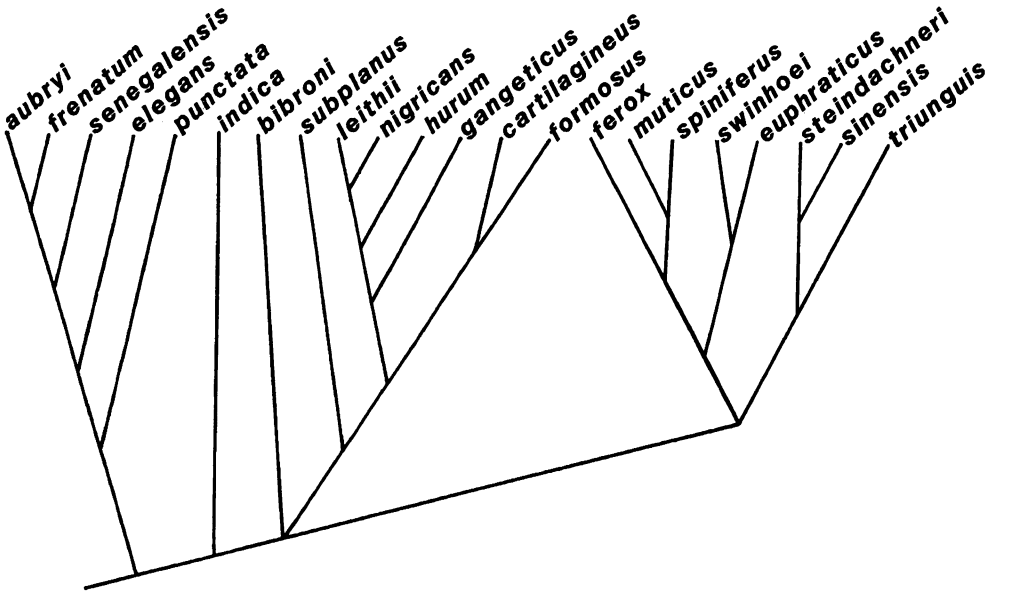

Fig. 1. A cladogram for the Trionychidae based on figure 50 in Loveridge and Williams (1957). *Trionyx emoryi,* which appears in the Loveridge and Williams figure, is currently considered to be a synonym of *T. spiniferus* (Webb, 1962) and is not included in the cladogram.

these states automatically form diagnoses. Recognition of the diagnostic features of monophyletic groups produces a strong hypothesis for the proper position of the Trionychidae among the Testudines and clarifies the interrelationships of its living species. In this work I have developed a hypothesis of cladistic relationships for the 22 Recent species of the family Trionychidae. The availability of large series of most living species and the completeness of Recent specimens has allowed a more complete character analysis than could be developed from fossils alone. A complete revision of the fossil members of the family lies beyond the scope of this study and will take many years to complete.

One of the most laudable aspects of phylogenetic analysis, which is absent from phenetic methods, is that it requires an observer to look beyond the taxa of immediate interest. Decisions about the polarity of character change in the ingroup (the Trionychidae) requires information from related forms. Therefore this study of the relationships of the members of a single family includes an investigation of interfamilial relationships and consequently has evolved into a study of representatives of the entire order. With its scope expanded by the requirements of phylogenetic methodology, this study has produced significant data on the distribution of character states among all turtles. These data are valuable in assessing the interfamilial relationships of trionychids.

The methodology employed also provides a means for identifying those characters which have states that appear to have been gained or lost independently, or which may have undergone reversal. These events, termed homoplasy, are the single most confounding feature in systematics. When systematic evaluations must be made from limited data sets, as in paleontology, it is important that characters subject to homoplasy are identified. Because most fossil Trionychidae have been described from shell material, an analysis of homoplasy in shell characters is critical to future work on the systematics of fossil forms.

The descriptive portions of this study focus entirely on characters significant in producing a phylogenetic arrangement for the ingroup. They are not meant as an exhaustive description of the osteology of the Trionychidae. Such a study has long been available (Ogushi, 1911).

The primary objectives of this project are to fill the largest remaining gap in our understanding of the phylogeny of living turtles by (1) determining the best placement of the Trionychidae within the Testudines; and (2) resolving relationships among the 22 extant trionychid species. In addition, this study will help provide a basis for future analysis of the relationships among the approximately 230 species known only from fossil material.

METHODS

THE PHYLOGENETIC METHOD

Systematics is not only a means of providing names for organisms and groups of organisms, but also a method by which we can infer and express the historical data of their descent. Biologists agree that all organisms have evolved by a single phylogenetic progression. The actual pedigree of taxa represents a succession of shared ancestries. Analysis of common ancestry can be a powerful explanatory tool for the distribution of traits of functional morphology (Lauder, 1982), ecology (Stearns, 1984), physiology (McNab, 1978), and behavior (Meylan and Auffenberg, 1986). But the possibility that any features are a result of shared common ancestry rather than more proximal causes cannot be explored unless classification reflects this single phylogenetic progression. Consequently, it is critical for systematists to propose classifications which reflect shared common ancestries. The cladistic method is explicit in its reliance on shared derived characters, which are a function of the descent of species.

The phylogenetic method relies on the identification and use of shared derived characters to discover recency of common ancestry. Given that parallelism is the exception rather than the rule, any two taxa are more likely to have a shared trait because it was present in their common ancestor rather than because it appeared independently on two occasions. Thus the distribution of shared derived characters among taxa can be used to build a hierarchical ranking of recency of common ancestry.

Developing this hierarchical ranking requires (1) identification of characters with appropriately distributed character states; (2) identification of primitive versus derived states for the characters; and (3) a system for the formulation of hypotheses of hierarchical relationship using the shared derived character data in the most efficient (parsimonious) manner.

Characters and Character States

The systematics of soft-shelled turtles has been based almost exclusively on skeletal morphology (see for example Baur, 1893; Siebenrock, 1902; Hummel, 1929; Stejneger, 1944; Loveridge and Williams, 1957; De Broin, 1977). Characters of the external soft anatomy are of little use, and few studies have employed them. The exceptions are the use of color pattern (Loveridge and Williams, 1957; Webb, 1962) and the presence of femoral and caudal valves in the Cyclanorbinae (most studies). For this reason, the character survey in the present study was restricted to skeletal morphology. A secondary advantage of this emphasis is future direct application of this study to the interpretation of the relationships of fossil trionychid species.

Characters of two types were sought: those uniform within the family but varying among higher taxa outside the family; and those varying among different groups of trionychid species. The former (interfamilial characters) provide a data set for hypotheses on the placement of trionychids within the Testudines. The latter (intrafamilial characters) provide a basis for developing phylogenetic hypotheses for species within the family Trionychidae.

Variation in a given character is treated as states of that character. Many of the characters used have only two states, such as presence or absence of a given bone, structure, or contact. Other characters include three or more discrete states or continuous variation. Multistate and continuous characters pose two methodological problems. First, for purposes of analysis it is necessary to divide a

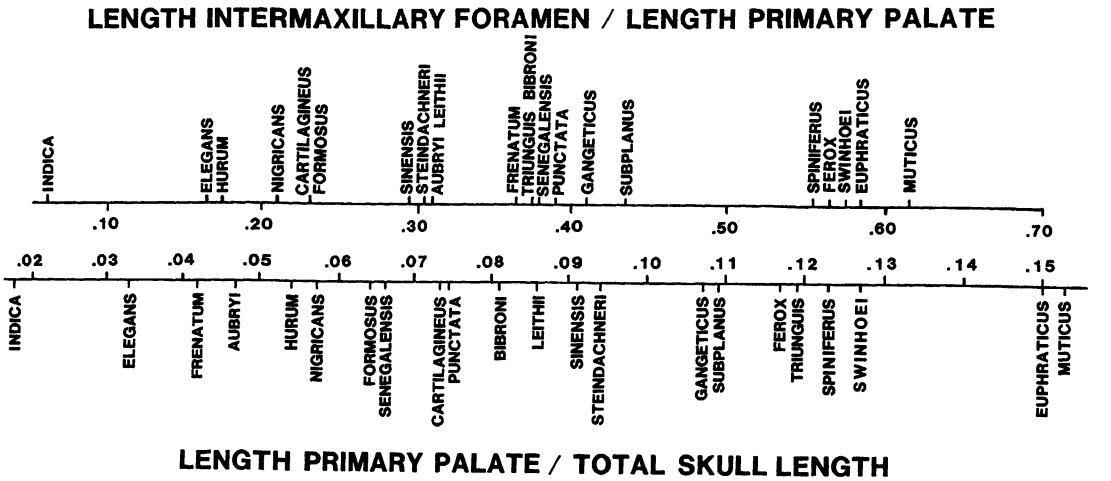

Fig. 2. Comparison of two continuous characters examined during the course of study of the variation in size of the foramen intermaxillaris. Foramen intermaxillaris/length primary palate falls into five discrete classes and is used in the cladistic analysis. Foramen intermaxillaris/total skull length shows no such discrete classes and could not be used.

continuously varying character into a number of discrete states. Secondly, it has been proposed (Gaffney, 1979a, personal commun.) that recognition of intermediate states requires ad hoc hypotheses that evolution has occurred in certain ways, and therefore multistate characters should be avoided.

Information contained in multistate characters, or morphoclines, is extremely useful for understanding the history of descent of any group (Maslin, 1952) and has been critical in formulating a hypothesis of relationships for trionychids based on the shell alone (Meylan, 1985). The multistate characters that have been used in the present study are of three types: (1) continuous characters of shape, size, relative position, etc., for which states have been determined by the occurrence of natural breaks along a continuum; (2) discrete characters of a meristic nature for which more than two possible states exist; and (3) two-state characters in which both states frequently occur in the same species, requiring the recognition of that third, intermediate condition. I submit that in all of these cases, as for two-state characters, only a hypothesis of character polarity is necessary. By invoking the principle of parsimony we can suggest that the degree of change required to arrive at a given state should be minimized, just as the number of postulated changes in a clade are ordinarily minimized by phylogenetic systematics. For example, we could propose that extreme reduction of peripheral bones in *Lissemys* occurs independently of complete loss of peripheral bones in all other trionychids (two steps) or that reduction in *Lissemys* is followed by complete loss in other trionychids (also two steps). But these two two-step changes are not equivalent. One requires two complete changes from an apparently very fixed primitive condition (loss of peripheral bones occurs otherwise only in *Dermochelys*); the other requires a single divergence from the primitive condition which is subsequently elaborated.

Multistate discrete characters (e.g., number of peripherals or neurals) present little problem for the recognition of different character states. Continuous characters of relative size must be divided into states by some artificial but objective means. As in other studies (Marx and Rabb, 1972; Drewes, 1984), I have divided continuous characters by plotting the average values for terminal taxa along a continuum, and employing natural breaks in distribution as evidence of various character states (see fig. 2, for example). If no natural breaks in distribution occurred, the character was discarded.

The characters employed in this study are given equal weight. Certain authors, most notably Hecht and Edwards (1977), have argued that some types of characters, for example those involving loss, should be given little weight. In this study characters are weighted only in the sense that they have been included or discarded, depending on the distribution of variation. I disagree with the concept of a priori character weighting in general, and in particular, I do not accept the supposition of Hecht and Edwards that characters involving loss are necessarily simple and subject to homoplasy, and therefore should be given low weight. The loss of a major structure such as the peripheral bones in turtles or the neural spine in snake vertebrae (a character of lowest value in the Hecht and Edwards' scheme) can occur only when a complex structural alternative (a character of highest value in the Hecht and Edwards' scheme) is available. The losses mentioned above require the development of strong and deeply sutured rib heads in the case of certain trionychoids, and relocation of numerous muscles that originate or insert on the neural spine in snakes. This may explain why complete loss of each of these features has apparently occurred only once. In both instances, loss is the immediately apparent result of a complex evolutionary event, and therefore should not be discounted.

There are two reasons for the inclusion of a maximum number of characters in this analysis. First, such inclusiveness is necessary to provide results that will be of greatest value to paleontology. Paleontologists are often faced with solving systematic problems on the basis of incomplete material. By increasing the number of characters, there is an increased likelihood that characters present in any given fossil will have been studied. The second reason is to provide three separate data sets to test the monophyly of problematic groups and detect homoplastic character states.

Because there are 113 characters discussed in this paper, some means of assisting the reader is required. Therefore, the characters are numbered. Characters 1–30 pertain to the shell, 31–78 pertain to the skull, and 78–113 pertain to the visceral skeleton and nonshell postcrania.

Character Polarity

Once the states of a given character have been recognized, it is essential to identify the primitive and derived extremes, or character polarity. Numerous criteria for determining the polarity of character transformations have been offered in the literature. The most often treated are outgroup comparison, commonality, evidence from the fossil record, evidence from embryology, and correlation of character states (Kluge and Farris, 1969; Marx and Rabb, 1972; Wiley, 1981). I follow Gaffney (1979a), Watrous and Wheeler (1981), and Wiley (1981) in relying on outgroup comparison as the best criterion for character polarity decisions. This criterion has been discussed at some length in recent systematic literature and methods have been outlined for making the most efficient use of outgroups when they are well established (global parsimony, Maddison et al., 1984), or when a number of outgroups could be the sister taxon to the ingroup (outgroup substitution, Donoghue and Cantino, 1984).

In this study I have employed data from all families of turtles and the arrangement of Gaffney (1984) to make use of the concept of global parsimony. That is to say, the outgroup for the Trionychidae is all other turtles. Decisions concerning polarity of characters within this family are most directly affected by the distribution of states within the Trionychoidea. The concept of the Trionychoidea is based on characters polarized at a higher level of universality.

Formulation of Phylogenetic Hypotheses

In my provisional arrangement of the Recent species of the Trionychidae based on 16 characters of shell morphology (Meylan, 1985), I conducted the search for the most parsimonious cladogram (that requiring the fewest evolutionary steps) by hand. As additional data have been assembled for this study I have partitioned them into three sets (shell, skull, and visceral skeleton plus nonshell postcrania). As each of these data sets became very large, it became necessary to employ a computer program to generate cladograms. I used Phylogenetic Analysis Us-

ing Parsimony (PAUP, version 2.3, 1984) by D. Swofford, which was made available through the Northeast Regional Data Center at the University of Florida.

PAUP emphasizes simple unrestricted parsimony procedures (Swofford, 1984). Its author finds that there is close correspondence between results obtained by hand and those generated via PAUP. One advantage in addition to the time-saving capabilities of PAUP is the MULPARS option. This option results in a listing of all "most parsimonious" trees. It seems certain that when working by hand one is unlikely to discover all such trees. The ability of the program to handle missing values improved its utility for use in the current project.

I have employed PAUP to formulate the most parsimonious hypothesis of relationship for the species within the family Trionychidae that can be derived from each of the three independent sets of osteological data. These are (1) 22 characters of the shell (an expanded version of Meylan, 1985); (2) 23 characters of the skull; and (3) 13 characters of the lower jaw and postcrania (exclusive of the shell). Additionally, an analysis of the three data sets combined was performed.

Comparison of Fundamental Hypotheses and Formulation of a General Hypothesis

Following the development of cladograms from the three separate data sets, it was desirable to formulate a single general cladogram from them and to compare the utility of various characters, especially those of the shell, in the formulation of this general hypothesis. Two methods, analysis of the three data sets in combination and a stepwise consideration of compatible characters, have been used for this procedure. Neither the Nelson (1979) method nor the similar Adams (1972) method produced a single, well-resolved cladogram of trionychid relationships.

BASIC TAXA

The species of living trionychid turtles recognized for this study are essentially those listed by Wermuth and Mertens (1961). The only differences are the use of the name *Trionyx swinhoei* for the large and colorful Chinese species which these authors had relegated to the synonymy of *Trionyx sinensis* (De Broin, 1977; Meylan and Webb, 1987) and the relegation of *Trionyx ater* to subspecific level within *T. spiniferus* (Smith and Smith, 1980). The 22 species used are the same as those employed in Loveridge and Williams (1957).

Two species recognized since the publication of Wermuth and Mertens (1961) have been deemed insufficiently distinct to be used in the current study. On the basis of the absence of integradation between *Lissemys scutata* and *L. punctata,* Webb (1982) proposed that the former be considered a full species rather than a subspecies of *L. punctata* (Annandale, 1912; Deraniyagala, 1939; Wermuth and Mertens, 1961). The primary morphological differences between the two are the configuration of the peripherals and the early development of plastral callosities in *L. scutata.* All superficial dermal callosities are highly variable within trionychid species, and thus additional, less variable features should be found to corroborate the validity of *L. scutata* before it is considered a distinct species. If *L. scutata* is distinct, there is little doubt that *L. punctata* is its closest relative.

The name *Trionyx nakornsrithammarajensis* was proposed for a "rare softshell" from Thailand (Wirot, 1979). Judging from the color pattern of the specimen in the figure included with the description, this name applies to *Trionyx cartilagineus.*

TERMINOLOGY

Taxonomy

Existing generic assignments are used for trionychids throughout the results and discussion sections of this paper. However, since the generic name *Trionyx* is currently used with about three-fourths of the species, little information is conveyed by the use of generic names. Therefore, specific epithets are used alone in figures and tables throughout.

Certain collective terms are used provisionally for groups of trionychid species throughout the text. They are used for groups which have been suggested to be monophyletic by more than one author. The Cyclanorbinae (Cyclanorbidae of Deraniyagala, 1939; or Lissemydinae, of Williams, 1950)

includes *Cyclanorbis elegans, Cyclanorbis senegalensis, Cycloderma aubryi, Cycloderma frenatum,* and *Lissemys punctata.* These species are considered to constitute a natural group in treatments by Deraniyagala (1939), Loveridge and Williams (1957), and Meylan (1985). The sister group of the Cyclanorbinae is the Trionychinae, which includes all noncyclanorbine members of the family. There is good evidence that the Trionychinae is a monophyletic group (Meylan, 1985). It has been recognized as such by Deraniyagala (1939), and Loveridge and Williams (1957). Within the Trionychinae two species groups have been treated as natural in all recent accounts: the four species of the Indian subcontinent (*Trionyx gangeticus, T. leithii, T. hurum,* and *T. nigricans*); and the three North American forms (*T. ferox, T. muticus,* and *T. spiniferus*) (Loveridge and Williams, 1957; De Broin, 1977; Meylan, 1985).

Names of familial and higher taxa of the Testudines are those suggested by Gaffney (1984). Monophyly of these taxa is not reexamined except for the superfamily Trionychoidea and its member families. The suffixes -oidea for superfamilies, -idae for families, and -inae for subfamilies are used consistently throughout the Testudines.

Morphology

Terminology for elements of the carapace and plastron follows Loveridge and Williams (1957). The concepts of Williams and McDowell (1952) concerning the homologies of the elements of the anterior lobe of the plastron are rejected. These authors suggest that the anterior midline element in trionychids is not the entoplastron, but rather a fused pair of epiplastra, and that the anteriormost paired elements are neomorphs which they term preplastra. On the basis of the sites of origin and insertion of the anterior trunk musculature, Bramble and Carr (MS) have shown that this is incorrect and that the anterior plastral elements in trionychids correspond to those of other turtles. The midline element is the entoplastron, and the anteriormost pair are the epiplastra. For skull and lower jaw terminology, I follow Gaffney (1972, 1979b), who has developed his glossary of skull morphology in part from Parsons and Williams (1961). A variety of sources is used for the nonshell postcrania: Williams (1950) for cervical vertebrae; Baur (1891a) and Zug (1971) for the pelvic girdle; and Schumacher (1973) for the hyoid.

RESULTS

VARIATION IN SHELL MORPHOLOGY

Thirty characters of the carapace and plastron have been determined to be useful for establishing inter- and/or intrafamilial relationships of trionychid turtles (table 1). They pertain to carapace size and shape, the nuchal region, the neural series, the shell periphery, posterior end of the carapace, and the plastron. Because of the unique nature of the shell of trionychids few of these characters are useful in testing proposed interfamilial relationships.

All character polarities discussed in this section are based on outgroup comparisons. It is therefore important that doubts about the homology of the shell of trionychids to that of other turtles be considered. Zangerl (1969) contended that the external bony layer in the Trionychidae and Dermochelyidae is composed of epithecal ossifications of more superficial origin than the dermal ossifications considered to form the shell in other turtles. This implies that the superficial layer of the shells of members of these two families are not strictly homologous to the same layer in other turtles. The existence of a nonhomologous superficial layer seems quite possible for *Dermochelys* in which there is total independence of the superficial bone and the deeper dermal elements of the shell (i.e., the ribs and neural spines of vertebrae). In cross section these "epithecal bones," which make up the superficial bony mosaic, lack dense layers on the external and internal surfaces (fig. 3, bottom). Thus they do not fit Zangerl's (1969) description of turtle shell bone of typ-

TABLE 1

Shell Characters and Character States Used for Resolving Phylogenetic Relationships of Recent Trionychid Turtles.

For each character the most primitive state is number 1

Characters	Character states
1. width/length of nuchal bone	1. less than 2 2. greater than 2 3. greater than 3 4. greater than 4
2. anterior and posterior costiform processes of nuchal bone united	1. no 2. yes
3. position of anterior edge of first body vertebra relative to nuchal bone	1. posterior edge of nuchal 2. middle of nuchal 3. anterior edge of nuchal
4. first and second neurals fused	1. no 2. yes
5. total number of peripherals	1. 22 2. 20 3. 14–18 4. 0
6. peripherals sutured to pleurals	1. yes 2. no
7. prenuchal bone	1. absent 2. present
8. size of eighth pleurals	1. large 2. reduced or absent
9. number of plastral callosities	1. seven 2. five 3. four 4. two 5. none 0. nine
10. hyoplastra and hypoplastra fuse just after hatching	1. no 2. yes
11. hyoplastra and hypoplastra fuse in adults	1. no 2. yes
12. fusion of xiphiplastra	1. absent 2. present
13. hypo–xiphiplastral union	1. xiphiplastra lateral to hypoplastra 2. hypoplastra lateral to xiphiplastra
14. number of neurals (fused 1 and 2 counted as 2)	1. nine 2. eight or nine 3. eight 4. seven or eight 5. seven or fewer
15. variability in position of neural reversal	1. always at same neural 2. always at adjacent neurals 3. highly variable
16. pleurals which meet at midline	1. eighth only 2. seventh and eighth or eighth only 3. sixth, seventh, and eighth or seventh and eighth 4. more than sixth, seventh, and eighth 0. none
17. point of reversal of orientation of neurals	1. at neural eight 2. at neural seven 3. at neural six or seven 4. at neural six 5. at neural four, five, or six
18. suprascapular fontanelles	1. closed at hatching 2. closed in large adults only 3. open throughout life
19. epiplastron shape	1. J-shaped 2. I-shaped
20. length epiplastra anterior to entoplastron contact	1. short 2. intermediate 3. long
21. depressions on eighth pleurals for contact of ilia	1. present 2. absent
22. shape of entoplastron	1. anterioposteriorly elongate or round 2. "boomerang-shaped"
23. bridge length	1. long 2. short
24. largest adult size 200 mm or less (disc length)	1. no 2. yes
25. carapace margin straight to concave posteriolaterally	1. no 2. yes
26. plastral buttresses reach across peripherals to contact pleurals	1. both axillary and inguinal 2. axillary only 3. neither
27. carapace sutured to plastron all across bridge	1. yes 2. no
28. rib heads strongly sutured to vertebral centra	1. no 2. yes
29. sexual dimorphism in disc length	1. no 2. yes
30. shell sculptured and lacking epidermal scutes	1. no 2. yes

TABLE 1—(*Continued*)

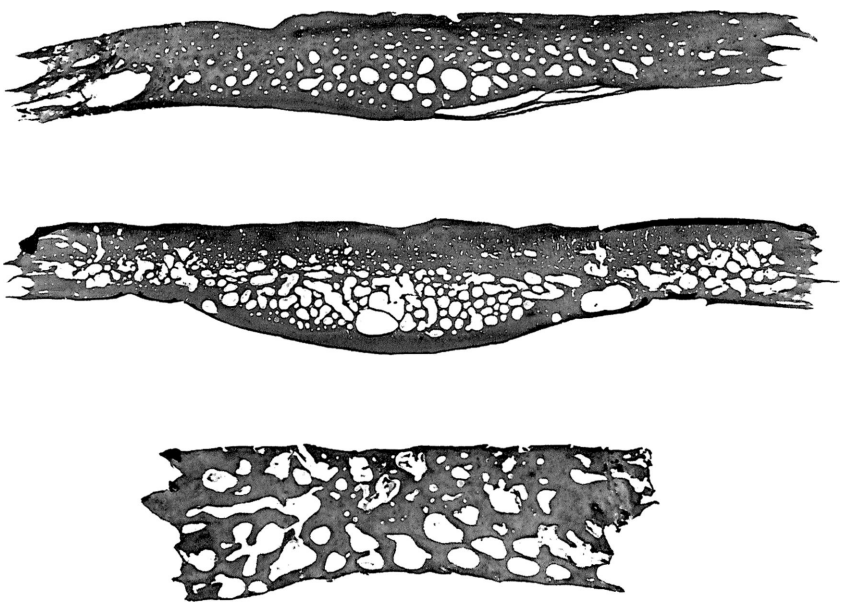

Fig. 3. Cross sections of single pleural elements of three cryptodiran turtles. **Top,** *Chrysemys picta* (UF 40615); **middle,** *Trionyx ferox* (UF 54212); **bottom,** *Dermochelys coriacea* (UF 37557).

ical dermal origin. The case is less clear for the most superficial bony layer in the Trionychidae. In members of this family, as in other turtles, there is complete correspondence between superficial bony elements and underlying deep dermal elements of the carapace. Furthermore, cross sections of either carapacial or plastral elements of trionychids reveal the presence of a spongy middle region with compact lamellar layers on either side (fig. 3 top, middle). This agrees with Zangerl's own description of typical dermal shell bone and fits Suzuki's (1963) description of the results of development of dermal shell bone in *Pseudemys scripta.* Zangerl's (1939) original argument for an epithecal origin of the superficial bone in trionychids is based on its delayed development rather than on its site of origin. The late development of the superficial layer does not have any clear bearing on the homology of its origin, and must yield to the physical evidence that, in cross section, trionychid shell elements do not differ significantly from other sectioned chelonian shells which are considered to be of normal dermal origin. Thus, unless other evidence can be provided, the superficial elements of trionychid shells may be regarded as homologous to those of other turtles.

Carapace Size and Shape

Even the smallest fragment of trionychid shell is immediately recognizable by its characteristic sculpturing. This sculpturing is never divided by scute sulci because scute sulci and the epidermal scutes they delineate, which are present on the shells of most other turtles, are always absent in trionychids. The only other living turtle which has a sculptured shell and lacks epidermal scutes is *Carettochelys.* The absence of epidermal scutes is considered to be a derived condition (character 30, table 8).

Recent trionychids are, for the most part, large turtles and many species approach one meter in total carapace length. The carapace consists of a bony disc with cartilaginous margins. In discussions of osteological material, including this one, it is the bony disc length rather than total carapace length which is used as an index of total size. The largest species of trionychids have bony discs over 500 mm in length; most reach disc lengths of 300 mm (table 2). The exceptions are few, and these are usually 200 mm or less in disc length.

Five species of *Trionyx* are small (under 200 mm disc length): *Trionyx muticus, T.*

TABLE 2
Maximum Size of Recent Trionychids (Character 24)

Species	Specimen	Length, bony disc (mm)
aubryi	BMNH 61.7.29	365
bibroni	BMNH 80.4.25.6	415
cartilagineus	ZSM 832/1920	316
elegans	NMW 1437	475
euphraticus	cited in Siebenrock, 1913	282
ferox	UF 45341[a]	371
formosus	cited in Annandale, 1912	274
frenatum	BMNH (Type of *Aspidochelys livingstoni*)	535
gangeticus	cited in Annandale, 1912	485
hurum	cited in Annandale, 1912	416
indica	MNHNP 1880-182	550
leithii	EOM 2819	380
muticus	UMMZ 128086	124
nigricans	cited in Annandale, 1912	403
punctata	cited in Deraniyagala, 1939	370
senegalensis	BMNH 1949.1.3.51	325
sinensis	ZSM 429/1911	201
spiniferus	UF 37228	186.5
steindachneri	MNHNP unnumbered	170
subplanus	calculated from skull BMNH 81.10.10.12	ca. 250
swinhoei	calculated from fig. 1A, Heude, 1880	490
riunguis	KNM-VP-ER-8123	410

[a] Allen (1982) reported an apparently larger *Trionyx ferox*.

spiniferus, T. steindachneri, T. sinensis, and *T. subplanus.* All of the carapacial discs of *T. subplanus* measured during the course of this study are under 180 mm, but one unusually large skull, BMNH 81.10.10.1 (figured as *T. cartilagineus* in Dalrymple, 1977), could have come from a specimen with a disc as large as 250 mm. Awaiting complete analysis of the relationship of head to shell size in this megacephalic form, *T. subplanus* is tentatively included among the smaller species. This list of diminutive forms agrees in part with a list assembled by De Broin (1977) based on skull size. Her inclusion of *T. leithii* and *T. ferox* as small forms was clearly an artifact of small sample size (see table 2).

Among other trionychoids, small size is common only in the Kinosternidae. Most known species of the Dermatemydidae and Carettochelyidae reach bony carapace lengths of 400–500 mm. Among the Kinosternidae the genus *Staurotypus* reaches adult sizes close to those of *Dermatemys* and *Carettochelys*; whereas *Claudius, Kinosternon,* and *Sternotherus* are smaller, usually under 200 mm. It seems likely that reduction in total size is a derived condition common to the Kinosterninae and that similar diminution occurred independently in one or more groups within the Trionychidae. Thus, small carapace size is considered to be a derived condition among trionychids (character 24, table 3).

Sexual dimorphism in total size is well known for turtles. In certain forms the male is larger and in others the female is larger. The latter occurs most frequently among aquatic emydids but also occurs in some trionychids. Webb (1962) provides data which indicate that all three North American forms are sexually dimorphic in size. This has not been shown for any Old World forms with the possible exception of *Chitra indica* (Wirot, 1979). Because of apparent absence among other trionychoids, sexual dimorphism, in which the female is larger, can be considered a derived feature within the Trionychidae (character 28, table 3).

The carapace of trionychids is unique among the Testudines in having a flexible margin. This margin varies in extent and thus in flexibility. In one species (*Lissemys punctata*) it makes up less than 10 percent of the total carapace length and contains bony elements which are most likely homologous to the peripherals of other turtles (fig. 4A; see discussion of character 5 under section on shell periphery). In other forms the cartilaginous margin makes up almost one-half of the carapace length (fig. 4B) and the bony disc is thus quite reduced.

There can be little doubt that reduction of the bony disc relative to the total carapace is a derived condition, as it occurs only within this family. However, variation in this condition among trionychid species shows no natural breaks and I have not been able to convert this continuous variable into a discrete one. It should be pointed out, however,

TABLE 3
Modal Character States for Shell Characters of the Recent Trionychidae Used in Analysis of Intrafamilial Relationships[a]

	Characters																					
Species	1	2	3	4	5	7	8	9	10	12	13	14	15	16	17	18	19	20	21	23	24	25	29
aubryi	2	1	2	1	4	1	1	1	2	2	2	2	1	2	1	1	2	1	1	1	1	2	1
bibroni	3	2	2	2	4	1	1	3	1	1	1	2	1	1	3	2	1	1	2	2	1	1	1
cartilagineus	3	2	2	2	4	1	1	2	1	1	1	1	1	1	2	2	1	3	2	2	1	1	1
elegans	2	2	2	1	4	1	1	4	2	1	2	2	1	2	1	1	1	1	2	2	1	1	1
euphraticus	3	2	2	2	4	1	2	4	1	1	1	3	1	2	3	2	1	1	2	2	1	1	1
ferox	3	2	2	2	4	1	2	3	1	1	1	3	3	2	4	2	1	1	2	2	1	1	2
formosus	2	2	2	2	4	1	1	3	1	1	1	1	1	1	2	1	1	1	2	2	1	1	1
frenatum	2	1	1	1	4	1	1	1	2	1	2	2	1	2	2	1	2	1	1	1	1	2	1
gangeticus	3	2	2	1	4	1	1	2	1	1	1	2	2	2	3	1	1	2	2	2	1	1	1
hurum	3	2	2	1	4	1	1	2	1	1	1	1	2	2	3	1	1	2	2	2	1	1	1
indica	3	2	3	2	4	1	1	3	1	1	1	1	1	1	3	1	1	1	2	2	1	1	2
leithii	3	2	2	1	4	1	1	2	1	1	1	2	1	1	3	1	1	2	2	2	1	1	1
muticus	4	2	2	2	4	1	2	1	1	1	1	2	3	2	4	3	1	1	2	2	2	1	2
nigricans	3	2	2	1	4	1	1	2	1	1	1	1	1	2	3	—	1	2	2	2	1	1	1
punctata	2	1	1	1	3	2	1	1	2	2	2	4	1	2	2	1	2	1	1	1	1	2	1
senegalensis	3	2	2	1	4	2	1	0	2	1	2	5	—	4	—	1	1	1	1	1	1	1	1
sinensis	4	2	2	2	4	1	1	1	1	1	1	2	3	2	4	2	1	3	2	2	2	1	1
spiniferus	3	2	2	2	4	1	2	1	1	1	1	3	3	2	4	3	1	1	2	2	2	1	2
steindachneri	2	2	2	2	4	1	1	3	1	1	1	2	1	2	2	1	1	3	2	2	2	1	1
subplanus	4	2	2	2	4	1	1	3	1	1	1	1	2	0	2	3	1	3	2	2	2	1	1
swinhoei	—	—	—	2	4	1	2	4	1	1	1	—	—	—	—	—	1	1	2	2	1	1	1
triunguis	3	2	2	2	4	1	1	3	1	1	1	3	1	2	3	2	1	1	2	2	1	1	1

[a] For descriptions of the characters and character states see table 1.

that cyclanorbines consistently have relatively larger discs than trionychines and in this respect they represent the more primitive condition.

Elsewhere (Meylan, 1985) I have suggested that the shell outline of *Cycloderma frenatum* is unique in having a sharply tapering rear half of the carapace with straight-to-concave posterolateral edges (compare fig. 4A to figs. 4B, 5A, and 5B). After examination of numerous carapaces of *Cycloderma aubryi* and *Lissemys punctata,* it is apparent that these species share the unique carapacial outline noted above. Other trionychids, like most other testudines, have round-to-oval shells that are convex posteriolaterally (character 25, table 3).

Nuchal Region

Dalrymple (1979) provides an excellent discussion of the role of the cervicodorsal joint in trionychids in allowing the retraction of a long neck into a small space. In order to accommodate such modification of this joint, the entire anterior portion of the trionychid carapace must have been extensively remodeled. In most cryptodires, the first thoracic vertebra is directly ventral to the first neural bone of the carapace (fig. 6A) and is firmly sutured to it. It is loosely jointed to the carapace and usually more anteriorly located in trionychids (fig. 6B–D). In *Lissemys* and *Cycloderma,* the first thoracic vertebra lies directly below the "preneural" to which it is weakly sutured, suggesting that the "preneural" is actually a first neural (see also Baur, 1893; Hay, 1908; Carpenter, 1981). The nuchals of *Lissemys* and *Cycloderma* are also the longest (relative to their width) among the trionychids (compare fig. 4A to figs. 4B, 5A, and 5B). Separate anterior and posterior costiform processes can be recognized (fig. 6B). Grooves for passage of the postzygapophyses of the eighth cervical vertebra are present on either side of the midline at the

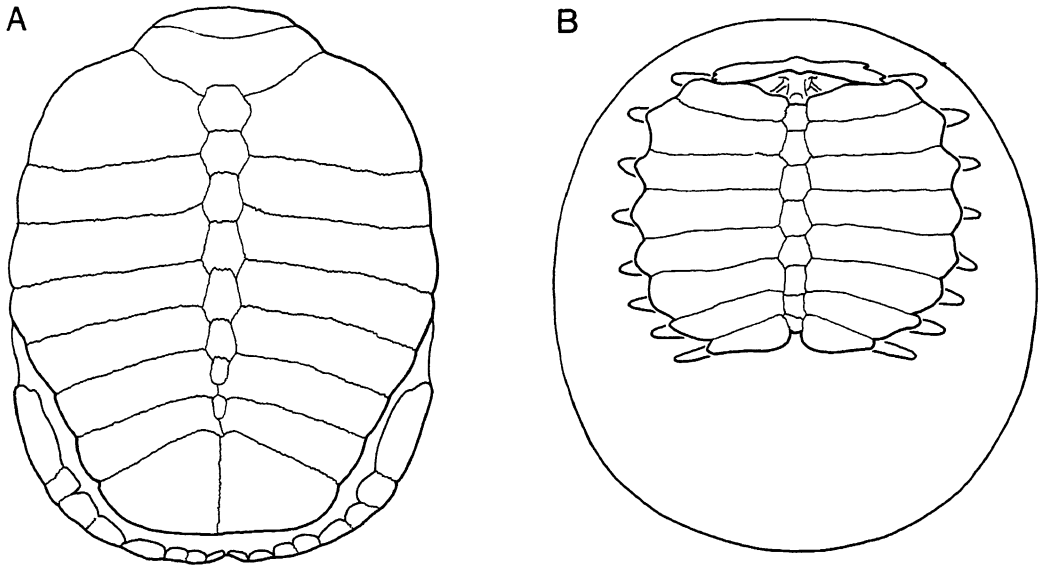

Fig. 4. Dorsal views of the carapace of two trionychid turtles. **A.** *Lissemys punctata* (UF 56017); **B.** *Trionyx subplanus* (MNHNP unnumbered, holotype, with details from BMNH 53.5.38).

base of the posterior costiform process. This combination of features places a well-fixed first thoracic vertebra well back from the edge of the carapace (fig. 6B). Among trionychids the condition in *Lissemys* and *Cycloderma* most closely approaches that seen in other cryptodires. Further derived conditions include less contact between the first thoracic vertebra and the first neural and more posterior placement of the nuchal such that it lies above the first thoracic vertebra.

An advanced condition of the nuchal region appears in *Cyclanorbis senegalensis,* in which the length of the nuchal bone is reduced, bringing the first thoracic vertebra closer to the anterior edge of the carapace. The anterior and posterior costiform processes of the nuchal are not clearly separate (as in figs. 6C, D), but the first neural (preneural) is still distinct from the second (as in figs. 4A and 5B). A similar condition is found in *Cyclanorbis elegans* and in *Trionyx gangeticus, T. leithii, T. nigricans,* and *T. hurum.*

Fusion of the first and second neurals occurs only when the first thoracic vertebra is free of overlying neurals due to reduction of the neural arch of the vertebra. It is present in all *Chitra, Pelochelys,* and Recent *Trionyx* other than the Indian forms: *T. hurum, T. leithii, T. nigricans,* and *T. gangeticus.* Up to about 10 percent of certain *Trionyx* species (*T. ferox, T. formosus, T. triunguis*) show separate first and second neurals.

The extreme of development in this suite of characters is found in *Chitra* (fig. 6D). In *C. indica,* prezygapophyses of the first body vertebra are immediately adjacent to the anterior rim of the carapace, and the nuchal is reduced to a narrow sliver of bone. Very narrow costiform processes occur on the anterior margin, and depressions which allow passage of the postzygapophyses of the eighth cervical are present just inside the rim of the carapace. In *Chitra* there is also a new pair of processes at the posterior edge of the nuchal. They can be distinguished from the posterior pair in *Cycloderma* and *Lissemys* by their position well posterior to depressions for passage of the postzygapophyses of the eighth cervical.

Variation in the nuchal region has been analyzed through the use of four characters (tables 1, 3). The primitive condition for nuchal shape (character 1) is that most similar to those of other turtles, that is, length equal to width or nearly so. Costiform processes (character 2) are not present in adult *Caret-*

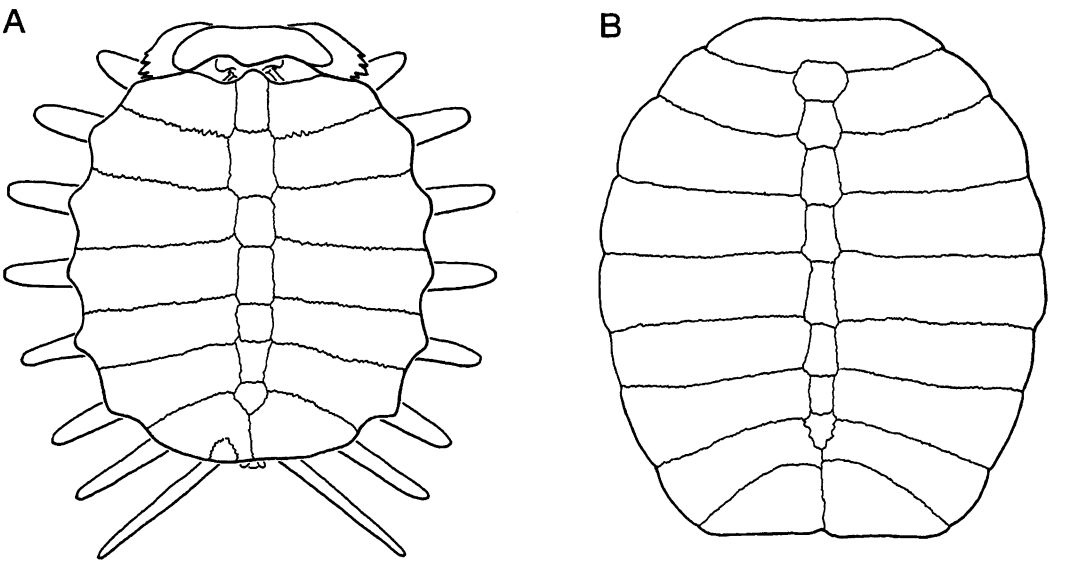

Fig. 5. Dorsal views of the carapace of two trionychid turtles. **A.** *Trionyx ferox* (AMNH 129737); **B.** *Trionyx hurum* (BMNH 86.8.22.2).

tochelys, but in some juveniles of the related genus *Anosteira,* there are two pairs (Bramble, personal commun.). In other trionychoids (Kinosternidae and Dermatemydidae) there is one pair in adults. But in newly hatched *Dermatemys* (BMNH 1984.1291) there are, in fact, two pairs. A cleared and stained hatchling *Sternotherus minor* and a skeletonized *Kinosternon flavescens* in the UF collection also have indications of paired processes anterior to a well-defined pair of costiform processes. Thus it seems likely that two pairs are present early in the ontogeny of all trionychoids. In the Dermatemydidae and Kinosternidae the anterior of the two pairs disappears with age while in the Trionychidae the two pairs occur separately in some forms (*Lissemys punctata* and both species of *Cycloderma*) and appear to be united in all others. Because this condition is probably present early in the ontogeny of all trionychoids, the possession of two pairs of costiform processes is considered primitive for trionychids.

Most cryptodires have the first thoracic vertebra at the posterior edge of the nuchal. As a result of apparent foreshortening of the nuchal in trionychids, the anterior edge of the shell comes to lie closer to the first thoracic vertebra. Close proximity of the anteriormost thoracic vertebra to the margin of the carapace is considered derived (character 3, table 3).

The trionychid "preneural" is here considered to be the first neural (see also Hasan, 1941). As suggested by Webb (1962) and Gaffney (1979c), fusion of the first neural to the second neural must be a derived character state (character 4). No nontrionychid member of the Trionychoidea always has two neurals between the first pleurals, but there are two in some *Carettochelys* (BMNH 1903.4.10.1). Furthermore, there are two thoracic vertebrae between the first pleurals of all trionychids. In *T. ferox* two neurals form (one on each of the first two thoracic vertebrae) and then fuse into a single element (Carpenter, 1981; present study).

The carapace of adult turtles is ordinarily a solid bony structure without openings or fontanelles. Peripheral fontanelles are not uncommon; they occur in juveniles of all cryptodires and are retained in some adult chelydrids, cheloniids, and trionychids. In trionychids, peripheral fontanelles are difficult to visualize because the peripheral bones

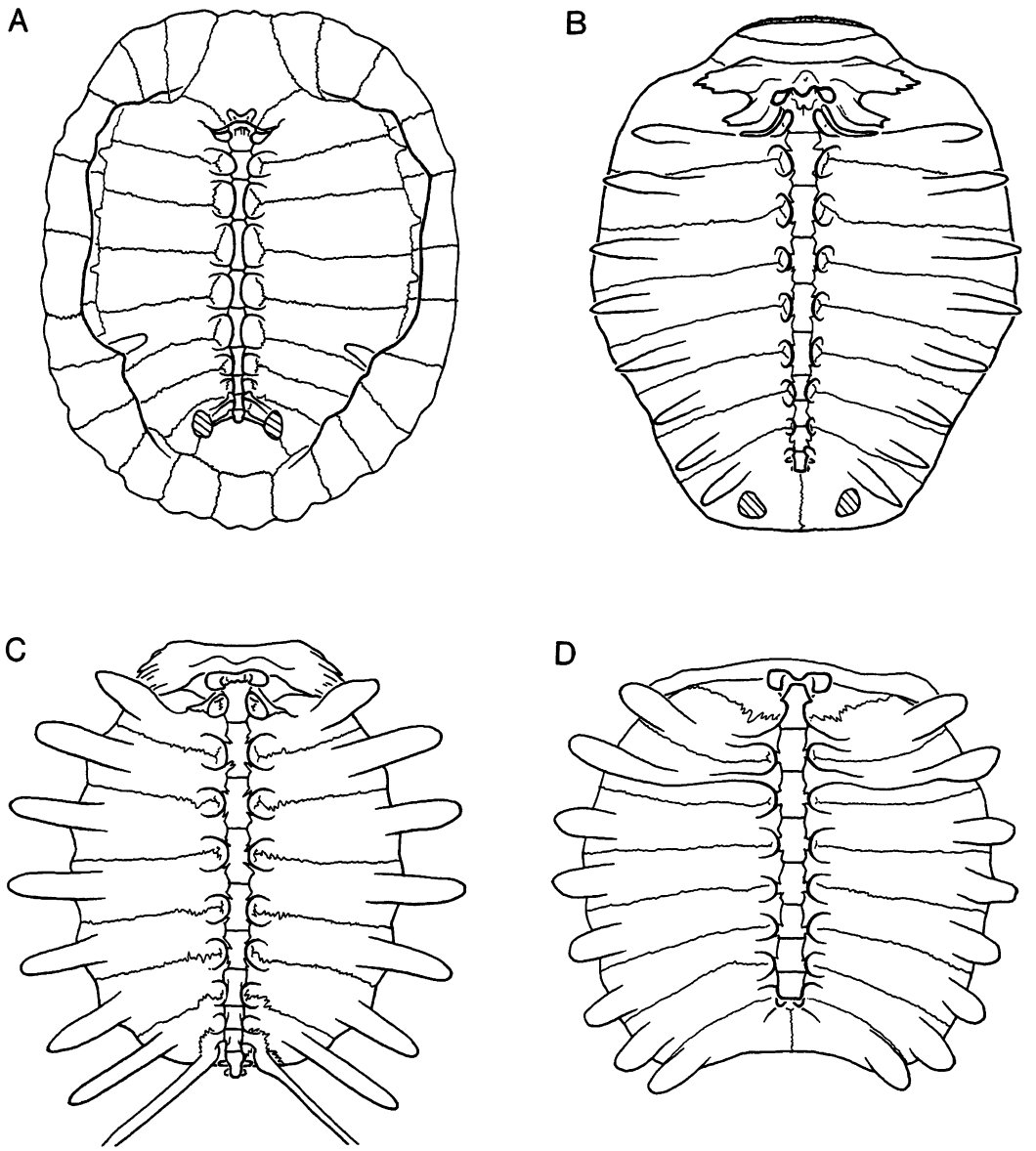

Fig. 6. Internal views of the carapace of four eucryptodiran turtles. **A.** *Trachemys scripta* (AMNH 111961); **B.** *Lissemys punctata* (UF 56017); **C.** *Trionyx ferox* (AMNH 129737); **D.** *Chitra indica* (MCZ 29487). Surfaces for ilial articulation are stippled.

are lacking. Fontanelles closer to the midline of the carapace are much less common. They occur above the ilia in very old individuals of some testudinoids (e.g., *Terrapene, Cuora, Gopherus, Homopus*) and some *Kinosternon,* and above the scapulae (=suprascapular fontanelles) in certain trionychids and at least one testudinid, *Homopus.*

Suprascapular fontanelles are probably present early in the development of all trionychids. They are closed at hatching in some forms (*Lissemys punctata*) but remain open

TABLE 4
Suprascapular Fontanelles (Character 18) in the Carapace of Recent Trionychids[a]

Species	A	B	C
aubryi	none	65.0	365.0
bibroni	71.0	200.0	415.0
cartilagineus	174.0	172.0	316.0
elegans	none	182.0	475.0
euphraticus	273.0	217.0	273.0
ferox	237.0	120.5	315.0
formosus	none	156.0	156.0
frenatum	none	180.0	535.0
gangeticus	106.0	205.0	460.0
hurum	none	132.0	292.0
indica	none	180.0	550.0
leithii	none	205.0	380.0
muticus	124.0	none	124.0
punctata	none	60.0	277.5
senegalensis	none	113.0	294.5
sinensis	140.0	117.0	242.0
spiniferus			
males	89.5	85.0	89.5
females	186.5	none	186.5
steindachneri	170.0	none	170.0
subplanus	177.0	none	177.0
triunguis	83.5	197.0	410.0

[a] Disc length (mm) for the largest specimens with fontanelles (A), smallest specimen without fontanelles (B), and largest specimen examined for fontanelles (C) are given for each species.

TABLE 5
Number of Neurals in Recent Trionychid Turtles[a]

Species	N	7	8	9	10
aubryi	17		0.71	0.29	
bibroni	10	0.10	0.20	0.70	
cartilagineus	18		0.17	0.78	0.06
elegans	14	0.21	0.43	0.36	
euphraticus	6		1.00		
ferox	31	0.06	0.88	0.06	
frenatum	5	0.20	0.20	0.60	
gangeticus	7		0.71	0.29	
hurum	5		0.20	0.80	
indica	13			1.00	
leithii	3		0.33	0.67	
muticus	7		0.43	0.57	
punctata	19	0.21	0.74	0.05	
senegalensis	17	0.18	0.06		
sinensis	25		0.40	0.60	
spiniferus	18	0.06	0.88	0.06	
steindachneri	3		0.33	0.67	
subplanus	10			0.80	0.20
triunguis	14		0.92	0.08	

[a] Values represent the frequency of occurrence for the sample. A fused first and second neural is counted as two elements. Seventy-six percent of *Cyclanorbis senegalensis* have 6 or fewer neurals. *Trionyx formosus, T. nigricans,* and *T. swinhoei* are excluded due to insufficient sample size.

throughout life in others (*Trionyx subplanus, T. spiniferus* [except some old males], *T. muticus,* and *T. steindachneri*). In most trionychids suprascapular fontanelles close up at some point between hatching and the attainment of adult size (table 4). However, insufficient data on the timing of closure in most species prevents the use of this character. Early loss of the fontanelles is likely the primitive condition and lifelong retention derived.

The Neural Series

The above argument suggests that the trionychid "preneural" of many authors is the first neural. Thus the most complete neural series in trionychids includes nine elements between the nuchal and eighth pleurals. The normal pattern in cryptodires is a continuous series of neurals from the nuchal to the suprapygal, with uniform orientation. All trionychids lack a suprapygal, and the eighth pleurals meet at the midline (except in *Trionyx subplanus*). The most complete series of nine neurals, with all or the majority (numbers 2–7) hexagonal and uniformly facing posteriorly (see below), is likely to be the most primitive condition among living trionychids.

Modification of the presumed primitive condition results from four apparently independent changes: (1) the fusion of the first and second neural (treated above, character 4), (2) interruption of the neural series by pleurals meeting at the midline (character 16), (3) variation in the number of neurals expressed on the dorsal surface of the carapace (character 14, table 5), and (4) variation in the location at which orientation of the neurals reverses (character 17, table 6). There are also interspecific differences in the amount of variability in the point of neural reversal (character 15). That is to say, in some species

TABLE 6
Location of Reversal in Neural Orientation in Recent Trionychids[a]

Species	N	4/5 or anterior	5	5/6	6	6/7	7	7/8	8
aubryi	17							0.12	0.06
bibroni	10			0.10	0.30	0.50	0.10		
cartilagineus	18				0.28	0.17	0.44	0.06	0.11
elegans	14								0.43
euphraticus	6			0.17	0.33	0.33	0.17		
ferox	31		0.16	0.13	0.19	0.32	0.19		
frenatum	5					0.20	0.40		0.20
gangeticus	7				0.57		0.43		
hurum	5				0.40	0.20	0.40		
indica	13				0.08	0.92			
leithii	3		0.33			0.33		0.33	
muticus	7			0.14	0.14	0.57	0.14		
punctata	19						0.32	0.11	
sinensis	25		0.08		0.08	0.12	0.28	0.40	0.04
spiniferus	18		0.28	0.11	0.33	0.06	0.17	0.06	
steindachneri	3						0.33	0.33	
subplanus	8						0.25	0.63	0.13
triunguis	14				0.08	0.69	0.08	0.15	

[a] Location of the most posterior reversal is given as a frequency of occurrence at or between neurals. Values which do not sum to 1.0 are due to individuals with no neural reversal (see table 7). *Trionyx formosus, T. nigricans,* and *T. swinhoei* are excluded due to insufficient sample sizes; in *Cyclanorbis senegalensis* the neural series is too fragmented to allow the detection of reversals.

the location of reversal is always at the same neural; in others, neural reversal occurs only at either of two adjacent neurals; and in still others, it may occur anywhere along the neural series.

Interruption of the neural series by pleurals meeting at the midline is not common among cryptodires. Most species have a neural series which is uninterrupted from the nuchal to the suprapygals. In dermatemydids and kinosternids, posterior pleurals may meet on the midline but in this case the posteriormost neurals usually do not appear and so they cannot be isolated from the anterior portion of the series. In *Carettochelys* pleurals often meet along the midline, isolating sections of the neural series. The neurals of *Carettochelys* are extremely narrow and thus appear to be less generalized than those of trionychids. Relying on global parsimony in establishing polarity in this case, I must consider the absence of pleural interruption of the neural series primitive for the Trionychidae.

Actually, interruption of the neural series is rare in trionychids. The last neural is isolated from the rest of the neural series in occasional specimens of *Lissemys punctata* (2 of 19), *Trionyx ferox* (5 of 31), *T. gangeticus* (1 of 7), and *T. hurum* (1 of 5). More frequent neural isolation occurs only in the two species of *Cyclanorbis*. Siebenrock (1902) discussed the marked variability of the neural series in these two species in his paper which established the existence of the two forms on osteological grounds. Both *Cyclanorbis* species can have long continuous rows of neurals or many isolated neurals. Although *C. senegalensis* tends to have more isolated neurals than *C. elegans,* the most reliable diagnostic features of these two species are found in the plastron. *C. senegalensis* is unique among living trionychids in possessing gular callosities. *C. elegans* is unique among cyclanorbines in having callosities of the fused hyo-hypoplastra that are flat or concave along their anterior edge.

The number of neurals appearing on the surface of the carapace in trionychids varies from 3 to 10. The occurrence of a tenth neural is very rare (3 of 242 specimens, two *Trionyx*

subplanus and one *T. cartilagineus*) and seems to be anomalous. Thus, nine neurals make up the most complete series, and the possession of nine neurals is considered to be the fundamental condition for trionychids. This is not supported by evidence from the outgroups. All other members of this superfamily have lost varying portions of the posterior neural series. This makes determining a primitive number based on the trionychoids alone quite difficult.

Looking outside of the Trionychoidea, one finds nine neurals commonly in the Chelydridae, where they are packed closely together posteriorly. In the Cheloniidae, *Chelonia mydas* and *Eretmochelys imbricata* frequently have two neurals between the first pair of pleurals, as is proposed to be primitive for trionychids (see, for example, fig. 8 in Deraniyagala, 1939). Other sea turtles have higher numbers of neurals but this is due to division of neural elements (Zangerl and Turnbull, 1955), and nine neurals may actually be the primitive number for these species as well.

Variation in the number of neurals among living trionychids is given in table 5. The number of neurals (character 14, tables 1, 3) is treated as five character states, with nine neurals considered most primitive and seven or fewer neurals most derived.

Nearly all neurals of trionychids are six-sided (see figs. 4, 5). Anterior and posterior ends of each neural contact adjacent neurals, the four lateral sides contact four adjacent pleurals, but the anterior and posterior pairs of pleural contacts are of unequal length, one usually being significantly longer than the other. In the anterior part of the neural series the shorter pleural contacts face posteriorly, but in the posterior part of the series (in most species) the shorter contacts face anteriorly. Thus, there is usually a reversal in orientation of these anterioposteriorly asymmetrical elements in every neural series.

Reversal of orientation occurs in two ways. More commonly it occurs via a four-sided neural (=a "diaphragmatic" neural of Hummel, 1929). The pair of pleurals adjacent to this four-sided neural contacts the two posterior-facing short sides of the next anterior neural, and the two anterior-facing short sides of the next posterior neural (fig. 5B, neural 7). The second and less common reversal occurs via two successive asymmetrical pentagonal neurals (fig. 4B, neurals 7 and 8). The anterior of the pair contacts an anterior short side of one of the next posterior pair of pleurals, while the posterior neural contacts a short posterior side of the preceding pleural on the opposite side.

In the presumed primitive neural arrangement, reversal of neural orientation, if it occurs at all, is posteriorly located. But in many forms, reversal occurs anteriorly and this is considered to be derived. Such reversal usually accompanies other changes from the primitive neural configuration. Reversals can occur from neural one through eight and multiple reversals are common in some species (treated separately as character 16; tables 6, 7). Where multiple reversals occur the location of the most posterior one is thought to indicate the degree of anterior migration of neural reversal. Data on location of neural reversal are treated as five states of character 17 (tables 1, 3), with the most anterior being most derived. Data on the amount of intraspecific variability in the location of the last neural reversal are treated via three states of character 15 (tables 1, 3), with the most variable being considered most derived.

Shell Periphery

With the exception of the Trionychidae, the margin of all testudine carapaces is solid. This is due to the presence of peripheral bones that form a complete ring around the carapace. In nearly all turtles this ring is composed of 22 peripheral elements, a nuchal and a pygal. Only in the Trionychoidea is there reduction and complete loss of these elements. In all kinosternids and *Carettochelys* there is one fewer peripheral on each side (total of 20). Peripherals 2 through 10 in *Carettochelys* are not sutured to the pleurals, which is also true for the only trionychid which retains bones in the periphery, *Lissemys punctata* (character 6, table 3).

The homologies of the bones in the periphery of the shell of *Lissemys* have been questioned by many authors. Boulenger (1889), Loveridge and Williams (1957), Zan-

TABLE 7
Number of Reversals of Orientation in the Neural Series of Recent Trionychids[a]

Species	N	0	1	2	3
aubryi	17	0.82	0.18		
bibroni	10		1.00		
cartilagineus	18		1.00		
elegans	14	0.57	0.43		
euphraticus	6		1.00		
ferox	31		0.66	0.31	0.03
frenatum	5	0.20	0.80		
gangeticus	7		1.00		
hurum	5		1.00		
indica	13		1.00		
leithii	3		1.00		
muticus	7		0.86		0.14
punctata	19	0.58	0.42		
sinensis	25		0.80	0.16	0.04
spiniferus	18		0.44	0.28	0.28
steindachneri	3	0.33	0.67		
subplanus	8		1.00		
triunguis	14		1.00		

[a] Number of reversals is given as a frequency. *Trionyx formosus, T. nigricans,* and *T. swinhoei* are excluded due to insufficient sample sizes; in *Cyclanorbis senegalensis* the neural series is too fragmented to allow the detection of reversals.

TABLE 8
Modal Character States for Shell Characters of the Recent Trionychidae Used in Analysis of Interfamilial Relationships[a]

	Character states						
Taxa	5	6	22	26	27	28	30
Trionychidae	3/4	2	2	3	2	2	2
Carettochelys	2	2	1	3	2	2	2
Claudius	2	1	1	3	2	1	1
Staurotypus	2	1	1	3	1	1	1
Kinosterninae	2	1	—	3	1	1	1
Dermatemys	1	1	1	2	1	1	1
Chelydridae	1	1	1	3	2	1	1
Platysternon	1	1	1	3	2	1	1
Cheloniidae	1	2	1	3	2	1	1
Emydidae	1	1	1	1	1[b]	1	1
Testudinidae	1	1	1	1	1	1	1
Pleurodira	1	1	1	1	1[b]	2	1

[a] For descriptions of characters and character states see table 1.

[b] Except in kinetic forms.

gerl (1969), and others have considered these bones to be neomorphic structures. Walther (1922), Webb (1982), and Meylan (1985) have treated the peripherals of *Lissemys* as homologs of the peripherals of other turtles. Although these elements are found in the carapace only posterior to the bridge and they lack one-to-one correspondence with the pleurals, there is other evidence which suggests that they are degenerated peripherals and not neomorphs. In cross section the peripheral ossifications of *Lissemys* are like those of other turtles in that they consist of two laminar layers of bone which converge distally (fig. 7). Between these two layers is cancellous bone. *Lissemys* peripherals differ from those of other turtles principally in the absence of the proximal portion. Unless some developmental constraint that results in the formation of V-shaped elements in the periphery of all turtle shells can be identified, it may be best to consider these details of morphology as evidence of homology.

Peripherals are found in the carapace of *Lissemys* only posterior to the bridge and are usually about 18 in number (Deraniyagala, 1939). Peripherals are absent in all other trionychids. The reduction and loss of bones in the periphery is clearly derived (character 5, tables 1, 3, 8).

Although the rib heads of each pleural bone normally reach the centrum of the corresponding thoracic vertebra, the contact is not always a strong one. Only in trionychids and *Carettochelys* among the Cryptodira have I found strong, interlocking sutures (character 29, tables 1, 8). Richmond (1964) has suggested that the peripheral bones of most turtles form a locking ring between the arched carapace and the plastron, which acts as a tension member. This keeps the shell from expanding laterally when a dorsoventral force is applied. It is possible that these strengthened contacts between the rib-heads and vertebral centra may be an alternative means of countering such forces. Thus the carapace of *Carettochelys* may be "preadapted" for the loss of peripherals.

Both *Lissemys punctata* and *Cyclanorbis senegalensis* possess a prenuchal that is an isolated element that lies above the neck, just anterior to the nuchal (character 6, tables 1, 3). The prenuchal is a neomorph not found in any other cryptodire, and its appearance is a derived condition.

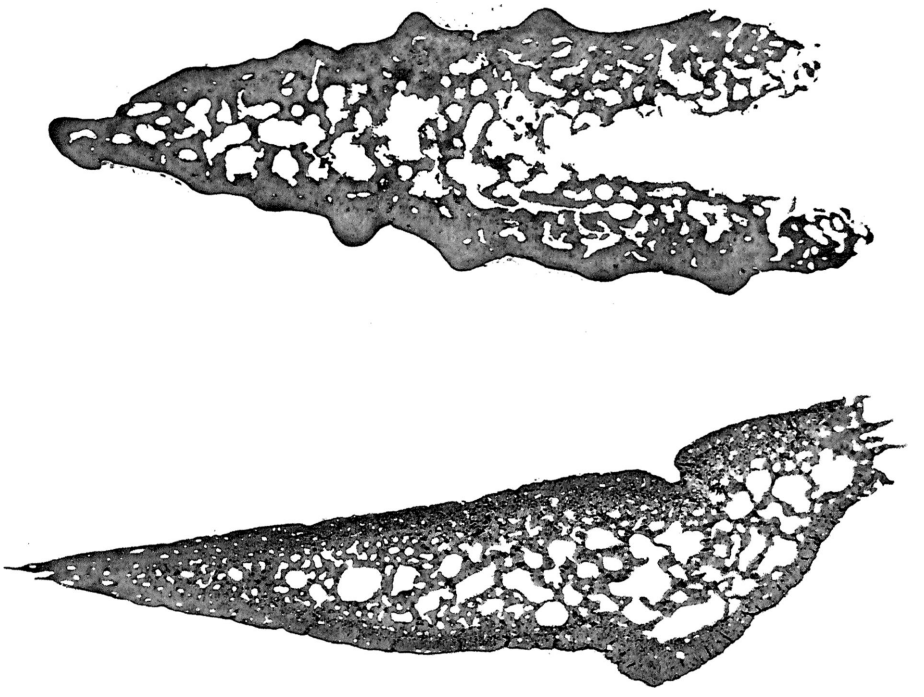

Fig. 7. Cross sections of a single peripheral of two cryptodires. **Top,** *Lissemys punctata* (UF 56017); **bottom,** *Chrysemys picta* (UF 40615).

Posterior End of Carapace

In nearly all turtles, the eighth and last pair of pleurals forms as significant a portion of the carapace as those which precede it. Although the eighth pleurals of trionychids develop allometrically, being relatively larger in adult turtles than in juveniles, it is still possible to detect a difference in their size among species (compare figs. 4 and 5). In some forms they are large, in others somewhat reduced, and in yet others they are absent. The presence of large eighth pleurals provides a complete complement of pleural bones. The reduction of this complete complement is considered to be derived. Large eighth pleurals are present in all cyclanorbines as well as all Old World trionychines, except *Trionyx euphraticus.* There is a trend toward the loss of the eighth pleurals in New World forms (character 8, tables 1, 3).

The ilia of cyclanorbines, except *Cyclanorbis elegans,* articulate with the eighth pleurals, as they do in other cryptodires. In all trionychines and in *C. elegans* the ilia articulate with the tough connective tissue just posterior to the end of the shell. The presence of distinct areas of contact (either depressions or tubercles) for the ilia on the eighth pleurals (fig. 6B) is considered primitive, their absence derived (character 21, table 3).

Plastron

The plastron of most cryptodires includes nine elements (one pair each of epi-, hyo-, hypo-, and xiphiplastra and a single entoplastron). These nine elements are usually well sutured to one another and form a solid bony structure. The same nine elements are present in all trionychids (Bramble and Carr, MS), but they are relatively incomplete; they are often not sutured to one another and do not result in a single solid structure. Where plastral sutures are present in trionychids they occur

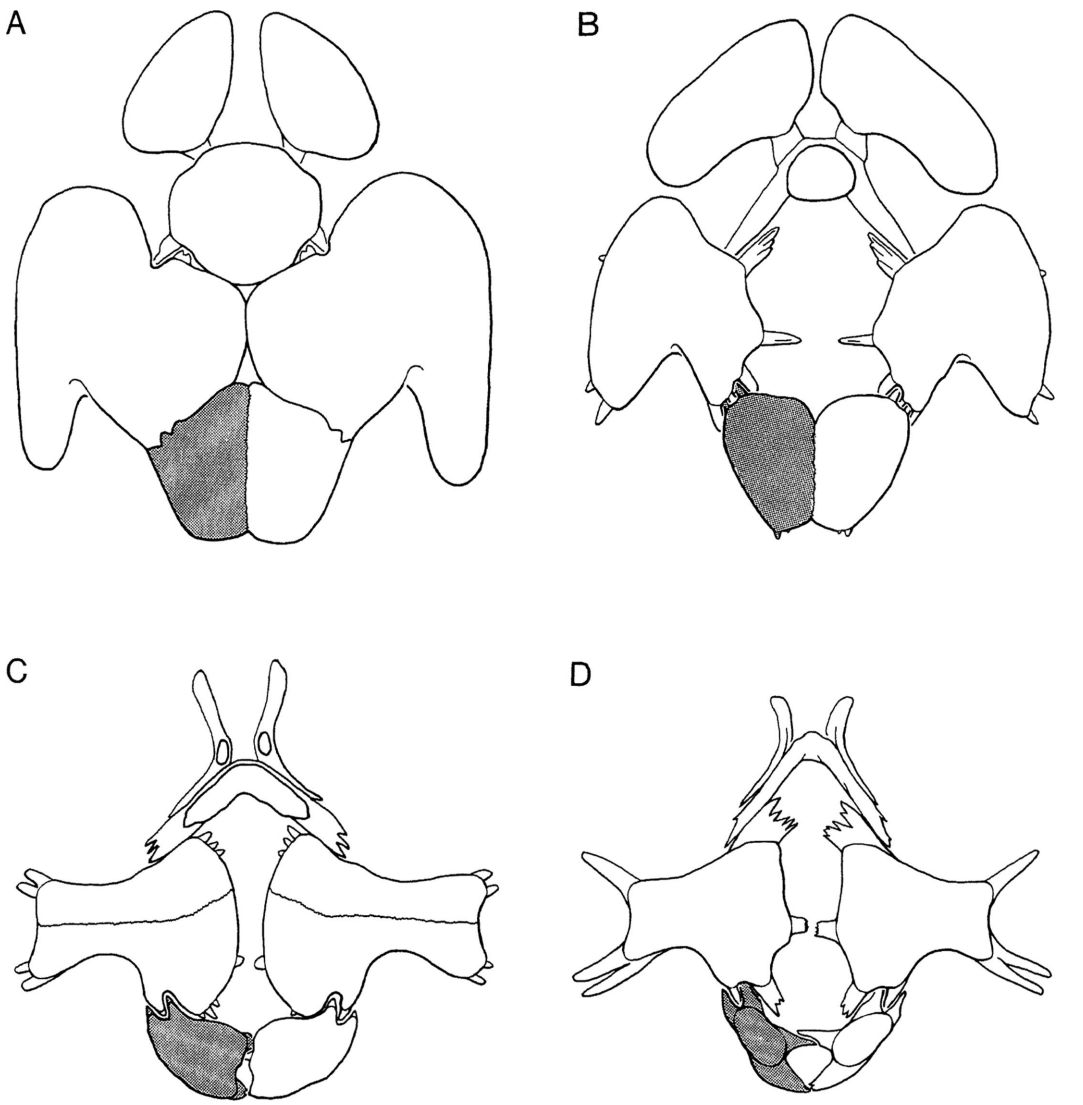

Fig. 8. Ventral views of the plastra of four trionychid turtles, with right xiphiplastra stippled. **A.** *Cycloderma aubryi* (MRAC 19212); **B.** *Lissemys punctata* (UF 56017); **C.** *Trionyx sinensis* (modified from Heude, 1880); **D.** *T. ferox* (AMNH 129737).

between the superficial dermal callosities with minor contributions from underlying elements. The presence of sutures, and thus of the callosities that allow them to occur, is interpreted as a primitive condition.

A suture is found between the hyo- and hypoplastra of all trionychids, and, in many, fusion occurs along this suture. The xiphiplastral callosities make contact at the midline in large *Lissemys, Cycloderma,* and *Trionyx,* but only in *Lissemys punctata* and *Cycloderma aubryi* does a sutured contact occur. This suture fuses in very old individuals of these two species. Sutures are absent between epi- and entoplastron, entoplastron and hyoplastra, hypo- and xiphiplastra, and along the midline (except for the xiphiplastra of the two species noted above) in all Recent trionychids.

The number of plastral callosities in all

trionychids increases with age but is stable in large adults (character 9). Callosities are present on all nine plastral elements in certain species and this is proposed as the primitive condition (fig. 8A, B). The callosities covering the hyo- and hypoplastron on each side are here considered to be a single structure making seven the primitive number. Seven callosities are found in *Lissemys, Cycloderma,* and some *Trionyx.* Derived conditions include both an increase and a decrease in the number of callosities (character 9, tables 1, 3). Only *Cyclanorbis senegalensis* has increased the number of callosities by the addition of a gular pair. The cyclanorbine *Cyclanorbis elegans* parallels the trend in the Trionychinae in having marked reduction in the number of callosities to two.

Although the fusion of two plastral elements is certainly derived, it can occur only when the primitive condition, a suture between two elements, is present. Thus the xiphiplastral suture in *Lissemys punctata* and *Cycloderma aubryi* suggests that they are primitive. However, xiphiplastral fusion is unique to these forms among trionychids and is considered a shared derived state (character 12, table 3).

Hyo-hypoplastral sutures occur at some stage in the ontogeny of all extant trionychids. Recent cyclanorbines share the common character state of hyo-hypoplastral fusion at a very small size (as small as 62 mm disc length). Fusion of the hypoplastra to the hypoplastra occurs in all adult *Trionyx ferox* (fig. 8D) and in adults of some populations of *T. triunguis.* Hyo-hypoplastral fusion is considered to be derived and to occur independently in cyclanorbines and trionychines (characters 10 and 11, tables 1, 3).

The xiphi-hypoplastral union in trionychids is of two types. In all trionychines the two anterior xiphiplastral processes lie on either side of the most lateral of the three posterior processes of the hypoplastron (fig. 8C, D). In cyclanorbines the two anterior processes of the xiphiplastron lie on either side of the middle of the three posterior processes of the hypoplastron (fig. 8A, B). The trionychine condition occurs in cheloniids, *Carettochelys,* and among kinosternids (*Kinosternon, Sternotherus,* and *Staurotypus*), suggesting that it is the primitive condition. Thus the presence of the hypoplastron lateral to the xiphiplastron at their junction is considered to be a derived condition unique to cyclanorbine trionychids (character 13, table 3).

Relative to the epiplastra of other Testudines those of trionychids are quite reduced in basic structure. The deep element, which may or may not be covered by a callosity, is I- or J-shaped. The J-shaped elements have a long ramus that is oblique to the midline and has a long contact with the entoplastron (fig. 8C, D). They also have an anterior projection of variable length that roughly parallels the midline. I-shaped elements consist of only the anterior portion and have minimal contact to the entoplastron (fig. 8B). J-shaped epiplastra are found in all trionychids except *Lissemys punctata, Cycloderma aubryi,* and *Cycloderma frenatum,* which have the alternate I-shape.

Long medial contact between the epiplastra and the entoplastron occurs in all nontrionychid turtles in which these elements are present. The posterior contact of the J-shaped epiplastra to the entoplastron maintains this contact and thus the J-shape is considered primitive, the I-shape derived (character 19, table 3).

The anterior extension of J-shaped epiplastra varies in length among the species in which it is found (compare fig. 8C and 8D). The extension beyond the entoplastron varies from 0.16 to 0.48 times the width of the hypoplastron of the right side (table 9). It is difficult to be certain which length of the extension is primitive for trionychids but it seems clear that the marked extension of *Trionyx cartilagineus, T. subplanus, T. sinensis,* and *T. steindachneri* is derived. As suggested by De Broin (1977), the species of the Indian subcontinent have epiplastra of intermediate length relative to the most elongate forms and other trionychids. Variation in this feature is treated as three states of character 20 with the longest extension considered to be most derived (character 20, table 3).

The boomerang shape of the entoplastron of trionychids is unique among turtles (character 22, table 8). Zangerl (1939) has implied that a T-shaped entoplastron is primitive for reptiles. The entoplastron in trionychids apparently arises from a proliferation and bend-

TABLE 9
Extension of the Right Epiplastron Beyond the Entoplastron, Relative to Total Hypoplastron Width of the Right Side (Character 20)[a]

Species	N	$\bar{x}$	1 S.D.
bibroni	3	0.165	0.042
cartilagineus	4	0.482	0.022
elegans	2	0.356	0.019
euphraticus	2	0.263	0.025
ferox	13	0.228	0.019
formosus	1	0.287	—
gangeticus	2	0.314	0.038
hurum	2	0.358	0.010
indica	5	0.230	0.011
leithii	3	0.312	0.021
muticus	3	0.183	0.017
senegalensis	3	0.280	0.015
sinensis	13	0.423	0.036
spiniferus	10	0.248	0.024
steindachneri	2	0.418	0.014
subplanus	5	0.479	0.039
swinhoei	1	0.221	—
triunguis	3	0.228	0.023

[a] Sample size, average, and one standard deviation are given for each species. Species with I-shaped epiplastra and *T. nigricans* are not included.

ing of the transverse portion of the T, combined with suppression of development of the longitudinal portion. The amount of bending of the transverse bar varies among trionychids and results in an angle of 62 to 122° between the two posteriolaterally directed rami. Variation within each species spans about 15°. Variation among species is quite continuous, with no natural breaks. Establishing a polarity for this character has not been possible because no other members of the Trionychoidea have similar entoplastron morphology. Difficulty in establishing polarity, combined with problems of variability, has made it impossible to include the angle of the entoplastron as a character in the intrafamilial analyses.

Plastral reduction in trionychids includes a marked reduction in the length of the bridge. Bridge length was compared to hypoplastron width as an index of this reduction. Bridge length varies from more than three-quarters of hypoplastron width (*Cycloderma aubryi*) to about one-eighth hypoplastron width (*Trionyx subplanus*). But variation falls into two discrete groups: those species in which the bridge is well over one-half hypoplastron width (fig. 8A, B), and those species with a bridge less than one-half hypoplastron width (fig. 8C, D). The former group includes all cyclanorbines except *Cyclanorbis elegans*; the latter includes all trionychines plus *Cyclanorbis elegans*.

Long plastral bridges occur in *Dermatemys* and *Carettochelys* but not in kinosternids. They are also long in testudinoids, with the exception of the most kinetic forms. Thus a long bridge is considered to be primitive, a short bridge derived (character 23, tables 1, 3, 8).

In addition to being short, the bridges of trionychid turtles lack ascending buttresses and sutured contacts to the elements of the carapace. Ascending processes cross the peripherals to contact the pleurals in both the axillary and inguinal regions in pleurodires and testudinoids except for those taxa with well-developed plastral kinesis. In *Dermatemys* only the axillary buttress reaches the pleurals. In all other living families the buttresses are quite reduced and do not cross the peripherals (character 26, tables 1, 8). The distribution of the states of this character can be explained about as parsimoniously by loss or by gain of buttress to pleural contact if only Recent forms are examined. However, buttress-to-pleural contact occurs in such extinct cryptodiran families as the Baenidae, Plesiochelyidae, and Meiolaniidae, suggesting that the presence of this contact is in fact the primitive condition.

In a few taxa that lack large plastral buttresses, the plastron is not strongly sutured to the carapace at the bridge. This occurs in chelydrids, cheloniids, *Claudius, Carettochelys,* and trionychids and is considered a derived condition (character 27, tables 1, 8).

VARIATION IN SKULL MORPHOLOGY

The value of the trionychid skull in systematics has been recognized by numerous authors (Gray, 1864, 1869, 1873a, 1873b; Boulenger, 1889; Hummel, 1929; Loveridge and Williams, 1957; De Broin, 1977). As pointed out by Loveridge and Williams (1957) there has been too much emphasis on the size and form of the jaws and too little on details of morphology and contacts of skull elements. Numerous authors have expressed

concern about the validity of characters of the size and shape of the jaws (Boulenger, 1889; Villiers, 1958; Barghusen and Parsons, 1966; Eiselt, 1976; De Broin, 1977). But only Dalrymple's (1977) account of variation in the skull of *Trionyx ferox* treats the correlation of skull size and shape to environmental factors in a detailed and systematic fashion. Dalrymple has found that the most variable features of size and shape of the skull of *T. ferox* are those which relate to feeding. Those structures which provide sites of origin or passage for jaw musculature increase allometrically with age, and the amount of relative increase is highly variable. Furthermore, the development of features related to feeding can occur independently of one another. This high degree of variability in characters of the feeding apparatus indicates that they are not useful systematic features, as had been suspected.

In this study quantitative characters of the jaws and associated structures (palatal groove, supraoccipital spine) are avoided. Treatment of the skull concentrates on contacts between elements and on contacts between elements and features of external morphology. Because complete interspecific comparison is the goal of this study, data from sectioned skulls (8 of 22 trionychid species available) will not be treated. This is the first study of trionychid systematics for which at least one skull of every currently recognized Recent species was available.

The skull characters and character states which are treated in this section are summarized in table 10. The details of distribution of the states of characters important for resolving relationships within the Trionychidae are given in table 11. The states for characters important for resolving interfamilial relationships are given in table 12. Character states which are autapomorphic for a living trionychid species are listed in table 13. Discussion of these characters is arranged by region of the skull beginning anteriorly and proceeding posteriorly, with the dorsal surface treated first.

Nasal Region

The premaxillae of cryptodires are usually paired elements that make up the ventral edge of the apertura narium externum (fig. 9B). Among trionychoids this is true only for dermatemydids and kinosternids. In *Carettochelys,* as well as all trionychids, these normally paired elements are fused to one another (character 44, tables 10, 12; figs. 9A, C, D, 10A, B). In trionychids this fused premaxillary differs further from those of the outgroups in being excluded from the apertura narium externum by the maxillae which meet dorsal to it (character 45, table 12; figs. 9A, C, 10A, B).

In three trionychids the premaxillary is either often absent (*Chitra indica,* 4 of 10), or nearly always absent (*Cycloderma frenatum,* 4 of 5; *Pelochelys bibroni,* 6 of 7) (character 65, table 11). The absence of this element is clearly derived.

Because nasals are absent in all trionychids, as they are in all living cryptodires (Gaffney, 1979b), the prefrontals are the anteriormost paired elements on the dorsal surface of the skull. Thus, the prefrontals form the dorsal border of the apertura narium externum. Laterally these elements contact the maxillae and border the anterior portion of each orbit between the maxilla and frontal. In most cryptodires the descending processes of the prefrontals contact the vomer and palatines. There is significant variation among trionychids in these contacts. There is also useful variation in the degree of emargination of the prefrontals at the dorsal edge of the apertura narium externum and in the degree of separation of the maxillae and frontals along the anterior margin of the orbit.

Through reduction of the prefrontals, vomer, and palatines, contact between the prefrontals and palatal elements in trionychids is greatly reduced, or lost. The prefrontal-palatine contact found in most cryptodires is lost in all trionychids (Gaffney, 1979b) and this loss can be considered a shared derived character for the family (character 38, table 12). Contact between the vomer and prefrontals is the common condition among trionychids, as it is for all testudines (fig. 10A). It is absent only in *Cycloderma aubryi, Cycloderma frenatum, Cyclanorbis senegalensis* and *Chitra indica* (fig. 10B), and is clearly a derived condition (character 36, table 11).

With the exception of two very primitive forms, *Proganochelys* and *Kallokibotion,* testudines have an unpaired apertura narium externum with a nearly straight to somewhat

TABLE 10
Systematic Characters and Character States of the Trionychid Skull

Characters	Character states
31. quadratojugal contacts maxillary	1. yes 2. occasionally 3. no
32. jugal contacts squamosal	1. no 2. in one-half of sample
33. quadratojugal contacts postorbital	1. yes 2. no
34. jugal contacts parietal on skull surface	1. no 2. in one-half of sample 3. yes
35. jugal contacts parietal within fossa temporalis	1. no 2. yes
36. vomer contacts prefrontal	1. yes 2. no
37. incisura columella auris closed	1. no 2. yes
38. palatines contact prefrontals lateral to vomer	1. yes 2. no
39. cheek emargination extends above lower edge of orbit	1. yes 2. no
40. anterior limit of cheek emargination formed by	1. maxilla 2. jugal
41. dorsal edge of apertura narium externum laterally emarginate	1. no 2. weakly 3. strongly
42. dorsal edge of apertura narium externum medially emarginate	1. no 2. yes
43. palatine forms a significant part of the lateral wall of the braincase	1. no 2. yes
44. premaxillae fused into single element	1. no 2. yes
45. premaxillae enter apertura narium externum	1. yes 2. no
46. basisphenoid contacts palatines	1. no 2. yes
47. foramen intermaxillaris	1. absent 2. present
48. vomer divides maxillae	1. yes 2. no
49. vomer reaches intermaxillary foramen	1. yes 2. no
50. vomer contacts pterygoid	1. yes 2. occasionally 3. no
51. vomer contacts basisphenoid	1. no 2. occasionally
52. processus pterygoideus externus projects from pterygoid	1. yes 2. no
53. size of foramen palatinum posterius	1. large 2. small 3. small and divided 4. many small openings
54. foramen palatinum posterius forms in	1. palatine and pterygoid and/or maxilla 2. palatine only
55. basis tuberculi basalis present	1. yes 2. no
56. foramen posterius canalis carotici interni completely within pterygoid	1. no 2. yes
57. canalis carotici interni straight and wide	1. no 2. yes
58. foramen jugulare posterius excluded from fenestra postotica by pterygoid arching to contact opisthotic	1. no 2. yes
59. foramen jugulare posterius excluded from fenestra postotica by descending process of opisthotic which reaches pterygoid	1. no 2. yes
60. foramen posterius canalis carotici interni relative to lateral crest of basioccipital tubercle	1. above 2. in it 3. below
61. groove for some portion of stapedial artery visible on prootic or descending process of parietal	1. yes 2. no
62. maxilla contacts frontal in front of orbit	1. no 2. yes
63. exoccipital contacts pterygoid	1. no 2. yes
64. basisphenoid shape	1. not medially constricted 2. occasionally medially constricted 3. medially constricted
65. premaxilla absent	1. no 2. occasionally 3. usually
66. vomer lost	1. no 2. yes
67. jugal contacts orbit	1. yes 2. no

TABLE 10—(*Continued*)

TABLE 10—(*Continued*)

Characters	Character states
68. epipterygoid, if present, contacts the palatine	1. yes 2. in ca. 50% 3. no
69. contact between pterygoid and foramen nervi trigemini occurs when epipterygoid is present	1. yes 2. no
70. when epipterygoid is present pterygoid contacts foramen nervi trigemini	0. between epipterygoid and quadrate or not at all 1. between prootic and epipterygoid or not at all 2. between epipterygoid and parietal or not at all
71. epipterygoid contacts prootic anterior to foramen nervi trigemini	1. no 2. in ca. 50% 3. yes
72. epipterygoid contacts prootic posterior to foramen nervi trigemini	1. no 2. yes
73. epipterygoid fuses to pterygoid	1. in subadults 2. in adults only 3. never
74. average ratio of intermaxillary foramen length to length primary palate	0. 0.07 1. about 0.20 to 0.40 2. about 0.60
75. postorbital bar relative to orbit	0. about 2 times orbit diameter 1. about equal to orbit to ⅓ of orbit 2. less than ⅙ of orbit
76. quadratojugal participates in processus trochlearis oticum	1. no 2. yes
77. quadrate make-up of the processus trochlearis oticum	1. greater than 50% 2. 33 to 50% 3. less than 33%
78. proportion of processus trochlearis oticum made up by parietal	1. 15.6% or less 2. 22.1% or more

anteriorly convex dorsal margin that is usually formed by the prefrontals (fig. 9B, D). This is true for the outgroups and for some living species of trionychids. The remaining trionychids show some degree of emargination of the prefrontals and thus alteration of this primitive shape of the external narial opening. With one exception emargination occurs laterally and is either shallow (fig. 9A) or quite deep (fig. 9B) (character 41, table 11). Only in *Cyclanorbis elegans* does emargination occur medially (character 42, table 13). The condition in *C. elegans* is considered to occur independently from that in other emarginate forms. Weak lateral emargination is considered to be intermediate between the strongly emarginate and nonemarginate conditions.

It is the prefrontal that normally separates the maxilla from the frontal at the anterior edge of the orbit in turtles. In a single trionychid, *Trionyx subplanus,* the maxillae contact the frontals lateral to the prefrontals in about one-half of the specimens examined. In the others, these elements are quite close and their proximity can be considered a unique feature of this species (character 62, table 13).

Orbital Region

A frequently used character in trionychid systematics is the relationship between the width of the postorbital bar and orbit diameter (character 75). The postorbital bar varies in width among the species of this family from two times wider than the orbit to one-sixth of orbit width (fig. 11). Variation in the width of the postorbital bar relative to the width of the orbit is not continuous but constitutes four separate sets of species. The outgroups vary in width of postorbital bar between state two (equal to or wider than orbit) and state three (one-half to one-third width of orbit). Only *Claudius,* with a very narrow postorbital bar (state 4), and *Platysternon* and the chelonioids, which lack temporal emargination (state 1), show the extreme conditions. In the current context it seems most appropriate to consider most divergent postorbital bar widths to be derived relative to the combined intermediate groups.

Skull Emargination

The advanced cryptodires (Chelomacryptodira of Gaffney, 1984), the Trionychoidea and Testudinoidea, have highly developed temporal emargination. But these two superfamilies differ greatly in the degree of cheek emargination that they exhibit.

As reviewed by Gaffney (1979b) there has always been a problem identifying landmarks

TABLE 11
Character States for Characters of the Trionychid Skull Useful in Assessing Intrafamilial Relationships[a]

	Characters																					
Species	32	34	36	41	48	49	53	54	58	59	60	64	65	68	69	70	71	72	73	74	75	76	78
aubryi	1	3	2	2	2	2	4	2	2	1	3	1	1	2	2	—	1	2	1	1	1	1	1
bibroni	1	3	1	1	1	1	2	1	1	1	2	1	3	3	1	0	2	1	2	1	1	1	1
cartilagineus	1	1	1	2	2	2	2	1	1	1	2	2	1	2	1	0	2	1	3	1	1	2	1
elegans	1	3	1	1	2	2	3	2	2	1	3	1	1	1	2	—	1	2	2	1	1	2	2
euphraticus	1	1	1	2	1	1	2	1	1	1	3	2	1	1	1	0	1	1	3	2	1	2	2
ferox	1	1	1	3	1	1	2	1	1	1	3	1	1	1	1	0	1	1	3	2	1	2	2
formosus	2	3	1	2	2	2	2	1	1	1	3	3	1	1	1	1	1	1	3	1	1	1	1
frenatum	1	3	2	1	2	2	4	2	2	1	3	1	2	3	2	—	1	2	2	1	1	2	1
gangeticus	1	1	1	2	2	2	2	1	1	1	3	3	1	1	1	1	1	1	2	1	1	2	1
hurum	1	2	1	3	2	2	2	1	1	1	3	3	1	1	1	1	2	1	3	1	1	1	1
indica	1	3	2	1	1	1	2	1	1	1	2	1	2	3	1	0	3	1	3	0	0	1	1
leithii	2	2	1	2	2	2	2	1	1	1	3	3	1	1	1	0	1	1	3	1	1	1	1
muticus	2	2	1	3	1	2	2	1	1	1	3	1	1	1	2	—	1	1	2	2	2	2	2
nigricans	2	1	1	2	2	2	2	1	1	1	2	3	1	3	1	1	1	1	3	1	1	1	2
punctata	1	2	1	1	2	1	2	2	2	1	3	1	1	2	1	1	1	1	1	1	1	1	1
senegalensis	1	3	2	2	1	1	3	2	2	1	3	1	1	3	2	—	1	2	1	1	1	1	1
sinensis	2	2	1	3	2	2	2	2	1	2	3	3	1	1	1	2	1	1	3	1	1	2	1
spiniferus	1	1	1	3	1	1	2	1	1	1	3	2	1	1	2	—	1	1	3	2	2	2	2
steindachneri	1	3	1	3	2	2	2	1	1	2	3	3	1	1	2	—	3	1	3	1	2	1	1
subplanus	1	2	1	3	2	2	2	1	1	2	3	2	1	1	1	—	1	1	2	1	2	2	1
swinhoei	2	1	1	2	1	1	2	2	1	1	3	1	1	1	1	0	1	1	3	2	1	2	2
triunguis	1	1	1	3	2	2	2	1	1	1	3	1	1	1	1	0	1	1	2	1	?	2	2

[a] Numbers refer to character states outlined in table 10.

suitable for making comparisons of emargination between taxa. The use of exposed elements seems to be most appropriate, but use of exposure of the postorbital as an index of temporal emargination in trionychids is problematical. All trionychids have very deep temporal emargination that leaves the processus trochlearis oticum fully exposed, and the communication of the fossa temporalis dorsalis with the fossa temporalis ventralis is

TABLE 12
States of Skull Characters Important in Interfamilial Analyses[a]

	Characters																		
Taxa	31	33	35	37	38	39	40	43	44	45	46	47	50	52	55	56	57	61	77
Trionychidae	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3
Carettochelys	1	1	1	2	1	2	1	2	2	1	2	2	2	2	2	2	2	2	2
Staurotypus	1	1	1	1	1	2	1	2	1	1	1	2	1	1	2	1	2	2	2
Claudius	1	1	1	1	1	2	1	2	1	1	1	2	1	1	2	1	2	2	1
Kinosternon	1	1	1	1	1	2	1	2	1	1	1	1	1	1	2	1	2	2	2
Dermatemys	2	1	1	1	1	2	1	2	1	1	1	1	1	1	2	1	2	2	3
Cheloniidae	3	1	1	1	1	2	2	1	1	1	1	1	1	2	1	1	1	2	2
Chelydridae	3	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Platysternon	1	1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Emydidae	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Testudinidae	2	1	1	2	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1
Pleurodira	3	1	1	1	1	1	3	1	1	1	1	1	3	1	2	1	1	2	—

[a] Numbers represent the character states listed in table 10.

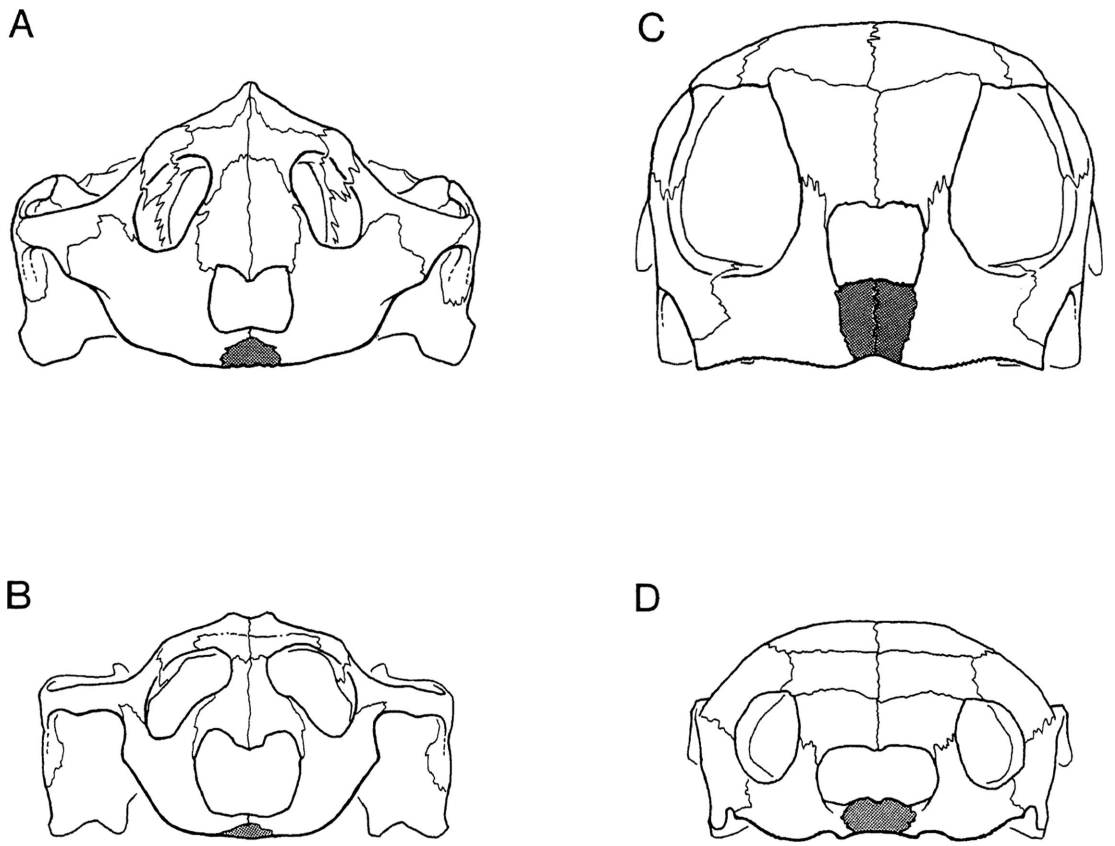

Fig. 9. Frontal views of the skull of four cryptodiran turtles showing fusion of the premaxillae (stippled) in trionychids (A, B) and carettochelyids (D), exclusion of the premaxillae from the apertura narium externum in trionychids (A, B), and slight (A) to extensive (B) emargination of the anterior border of the prefrontals. **A.** *Trionyx cartilagineus* (RH 129); **B.** *T. ferox* (AMNH 129737); **C.** *Chelonia mydas* (UF 55880); **D.** *Carettochelys insculpta* (UF 43888).

visible over a significant distance. With this degree of temporal emargination the postorbital bone, which makes up a significant portion of the postorbital bar, is usually exposed. This is true for all outgroup trionychoids and testudinoids examined. The postorbital in trionychids is one of several skull elements which has undergone extreme reduction. This reduction is so extreme that contact between the jugal and parietal occurs below the skull surface in all trionychids (character 35, table 12) and these two elements make up much of the postorbital bar. In some trionychids jugal-parietal contact is so strong that it is present on the skull surface and the postorbital is isolated from the temporal emargination (fig. 11A, B). Isolation of the postorbital from the temporal emargination might seem quite primitive and it certainly is if isolation is via parietal-squamosal or parietal-squamosal-quadratojugal contact. But isolation via jugal-parietal contact is a derived feature found only among trionychids. Jugal-parietal contact on the skull surface can vary within a single trionychid species. This variable condition is considered to be intermediate between the primitive absence of jugal-parietal contact on the skull surface and its presence which is certainly derived (character 34, table 11).

Lateral to the temporal emargination in trionychids is a very narrow bar formed by the jugal and quadratojugal. The trionychids parallel the condition seen in some emydids

TABLE 13
Autapomorphic Skull Features of Trionychid Turtles

Character	Species	Autapomorphic state
42	*Cyclanorbis elegans*	apertura narium externum medially emarginate
46	*Trionyx euphraticus*	basisphenoid fails to contact palatines
51	*Pelochelys bibroni*	vomer contacts basisphenoid
62	*Trionyx subplanus*	maxillae contact frontals in orbit
63	*Trionyx triunguis*	pterygoid isolated from exoccipital by basioccipital
66	*Cycloderma frenatum*	vomer is absent
67	*Cycloderma aubryi*	jugal excluded from orbit
74	*Chitra indica*	foramen intermaxillaris quite reduced
75	*Trionyx subplanus*	postorbital bar one-ninth of orbit diameter

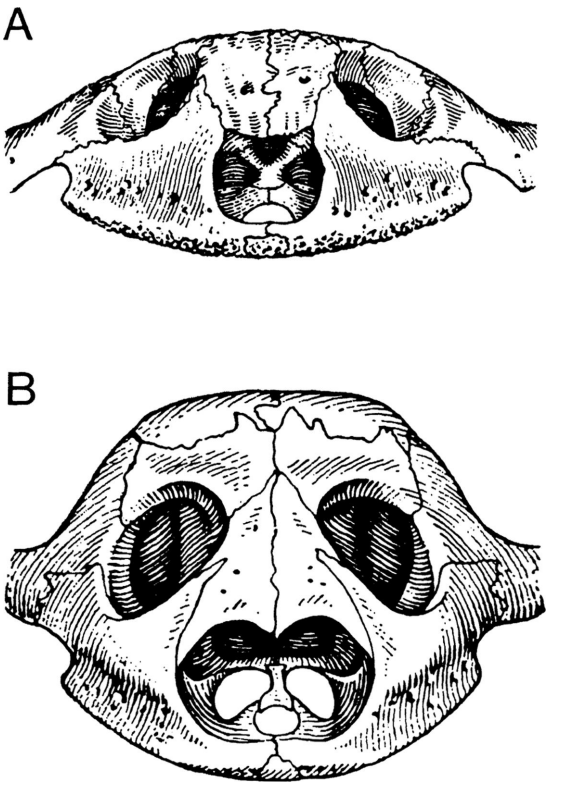

Fig. 10. Anterior view of the skulls of two trionychid turtles. **A.** *Trionyx triunguis* (BMNH 1947.3.6.12); **B.** *Cyclanorbis senegalensis* (BMNH 65.5.9.20); both from Loveridge and Williams (1957).

of extreme quadratojugal reduction. But unlike the case in emydids this element is never lost. In all trionychids the quadratojugal contacts only the jugal and not the maxilla or postorbital anteriorly. Posteriorly it sutures to the quadrate and squamosal. In other living trionychoids the contact of the quadratojugal to the postorbital is maintained and the quadratojugal maxillary contact is maintained except in some *Dermatemys* (UF 29168; fig. 172 in Gaffney, 1979b). Reduced contact of the quadratojugal is considered derived within the Trionychoidea (characters 31 and 33, table 12).

Because of the reduced size of the quadratojugal, the jugal and squamosal lie quite close to one another in all trionychids. In six species they are occasionally in contact. This is considered to be a derived condition (character 32, table 11).

Strong cheek emargination, which accompanies temporal emargination in testudinoids, is not found among living trionychoids. Although cheek emargination is visible in *Dermatemys, Carettochelys,* and kinosternids, it does not extend above a line extending horizontally from the lower edge of the orbit (character 39, table 12). In testudinoids, on the contrary, cheek emargination is quite well developed and extends well dorsal to such a line (except in *Malayemys*). In all testudinoids and trionychoids except for the Trionychidae, cheek emargination is limited anteriorly by the maxillary. In the Trionychidae, cheek emargination occurs within the jugal when it is present (character 40, table 12). Because of flexure of the snout in trionychids, ventral emargination of the jugal does reach above the lower rim of the orbit in a few cases. But emargination occurs only within the jugal and is the site of origin of the M. zygomatico-mandibularis (Dalrymple, 1977), a muscle which is unique to trionychids. Therefore, it is likely that cheek emargination in trionychids is not homologous to that of other turtles and that restriction of true cheek emargination ventral to the lower

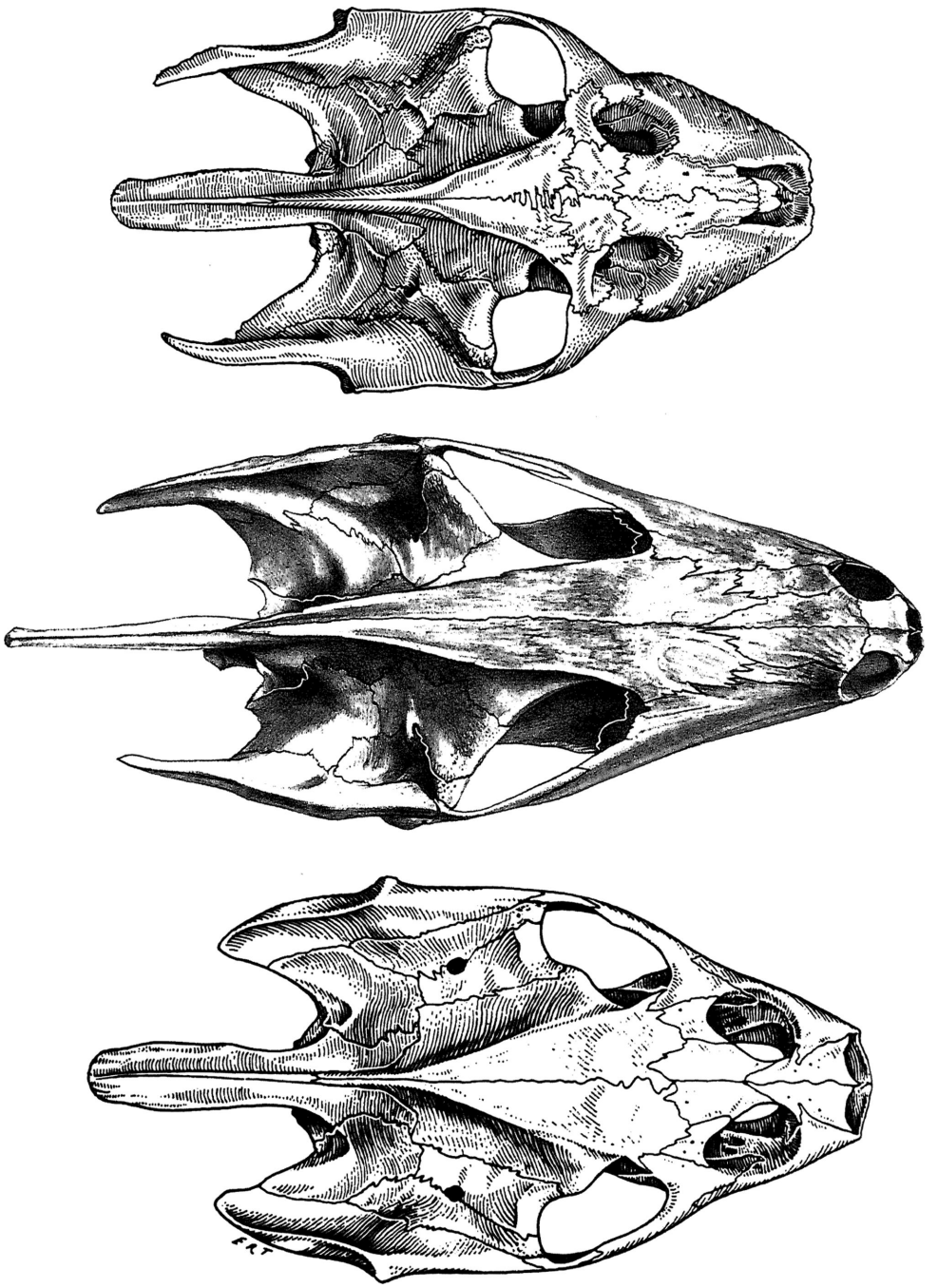

Fig. 11. Dorsal view of the skulls of three trionychid turtles. **Top,** *Trionyx triunguis* (BMNH 1947.3.6.12), from Loveridge and Williams (1957); **middle,** *Chitra indica* (from Gray, 1855, presumably BMNH specimen, sutures added from MCZ 29487); **bottom,** *Cyclanorbis senegalensis* (BMNH 65.5.9.20), from Loveridge and Williams, 1957).

TABLE 14
Average Contribution of Quadratojugal, Quadrate, Prootic, and Parietal to the Processus Trochlearis Oticum of Recent Trionychid Turtles

Species	N	Quadratojugal	Quadrate	Prootic	Parietal
aubryi	8	0.000	0.227	0.607	0.166
bibroni	7	0.000	0.207	0.602	0.117
cartilagineus	7	0.007	0.239	0.655	0.139
elegans	5	0.011	0.236	0.565	0.221
euphraticus	9	0.020	0.166	0.557	0.266
ferox	11	0.032	0.290	0.396	0.260
formosus	4	0.000	0.294	0.635	0.071
frenatum	4	0.026	0.130	0.734	0.136
gangeticus	7	0.007	0.137	0.720	0.144
hurum	6	0.000	0.213	0.744	0.054
indica	8	0.000	0.312	0.626	0.062
leithii	3	0.000	0.249	0.684	0.091
muticus	5	0.027	0.072	0.581	0.320
nigricans	1	0.000	0.200	0.500	0.292
punctata	6	0.000	0.192	0.717	0.094
senegalensis	6	0.000	0.177	0.671	0.152
sinensis	9	0.005	0.154	0.728	0.122
spiniferus	8	0.019	0.262	0.527	0.225
steindachneri	1	0.000	0.180	0.819	0.000
subplanus	6	0.088	0.180	0.625	0.112
swinhoei	1	0.033	0.100	0.500	0.300
triunguis	10	0.004	0.189	0.584	0.223

rim of the orbit can be considered a derived feature of the Trionychoidea (character 39, table 12).

Stapedial Foramen

The most significant difference between testudinoid and trionychoid turtles is in the pattern of blood flow to the head (McDowell, 1961; Albrecht, 1967; Gaffney, 1975, 1979b). This is reflected in variation of the size of the stapedial foramen and in the morphology of the prootic and parietal adjacent to this foramen. In testudinoids the majority of anterior blood flow is via the stapedial artery. Therefore the foramen stapediotemporale is large and there is often a groove in the prootic and parietal for the large stapedial artery. In trionychoids, the stapedial artery is reduced because most of the anterior blood flow is via the internal carotid artery. In this superfamily the foramen stapediotemporale tends to be reduced or absent and rarely is there evidence of a groove for the stapedial artery on the prootic or parietal (character 61, table 12). These features are important at the family level, there is little variation within the Trionychidae.

Processus Trochlearis Oticum and Quadrate

The processus trochlearis oticum is a distinctive feature of the Cryptodira. It is over this structure that the majority of the jaw adductor musculature lies. This is in contrast to the condition in Pleurodira in which the lower jaw adductors slide over a process of the pterygoid. In most cryptodires the majority of the processus is formed by the quadrate.

In trionychids the processus trochlearis oticum can be quite large and always involves the quadrate, prootic, and parietal (table 14). In 13 species the quadratojugal is included in at least some individuals (fig. 11 top). Within the Trionychidae, three useful patterns of variation are noted: the inclusion of the quadratojugal in the processus trochlearis oticum, reduction in the contribution made by the quadrate, and increase in the contribution made by the parietal. The first occurs when the quadratojugal sends a medial process across the anterior edge of the quadrate (fig. 11 top). It results in reduction of the quadrate contribution and is absent from all outgroups. It is thus considered to be derived within the Trionychidae (character 76, table 11). In trionychids, unlike essentially all other cryptodires, the quadrate makes up less than one-third of this structure (character 77, table 12).

There is additional variation among trionychids in the amount of parietal contribution. In the majority the parietal contribution is small, always less than one-sixth of the total (table 14). In the North American forms, and also *Cyclanorbis elegans, Trionyx euphraticus, T. nigricans, T. swinhoei,* and *T. triunguis* the parietal contribution is slightly larger, about one-fourth or more of the processus trochlearis oticum (character 78, table 11). The contribution of the parietal to this structure in other cryptodires is quite limited or absent. Thus the large contribution in trionychids is clearly derived.

In very few chelonians does the quadrate

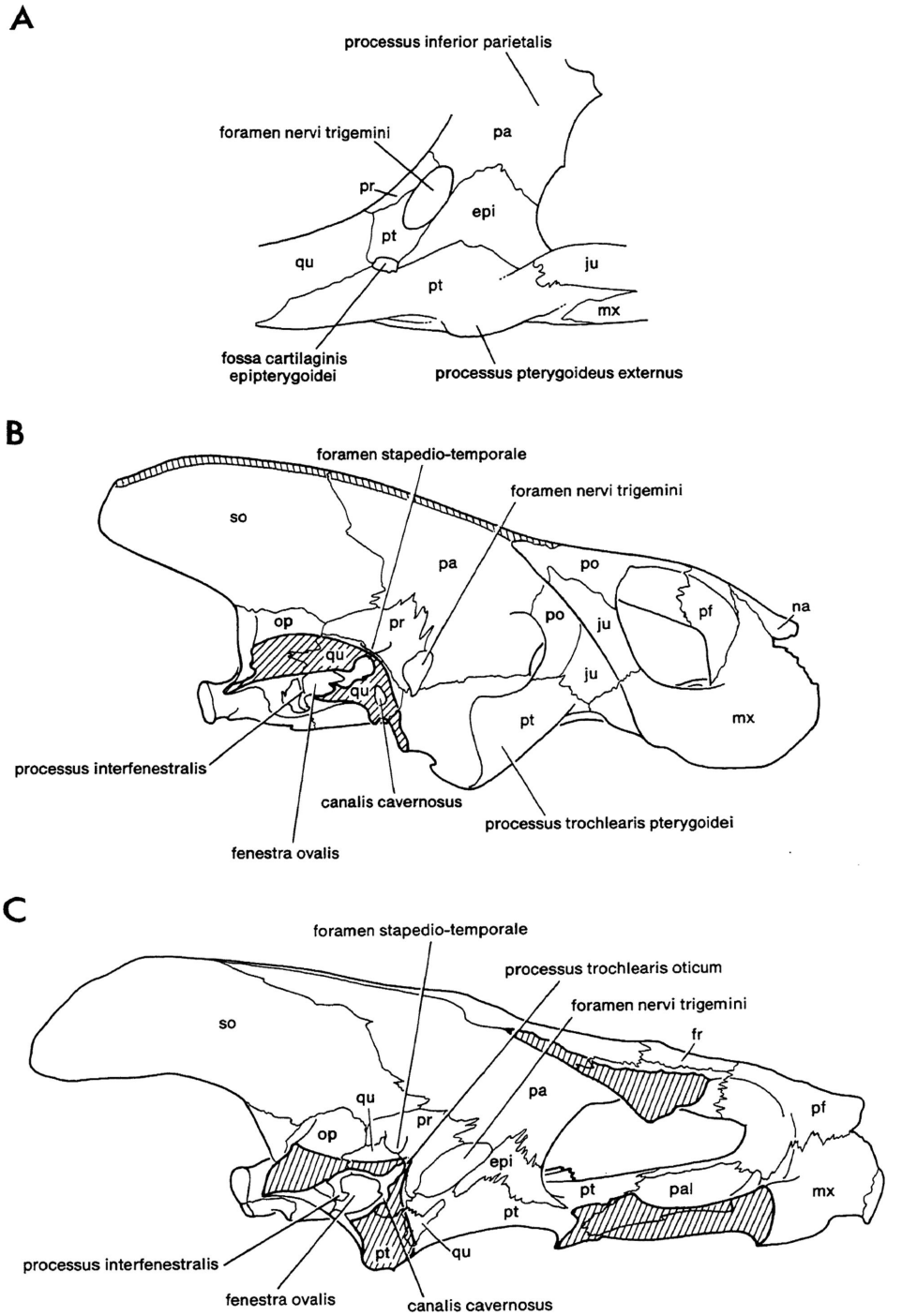

Fig. 12. Right lateral views of the skull of three cassichelydians with portions removed to expose trigeminal region. **A.** *Solnhofia parsoni* (Teyler Museum 4023); **B.** *Emydura* sp. (AMNH 72418); **C.** *Chelydra serpentina* (AMNH 9249).

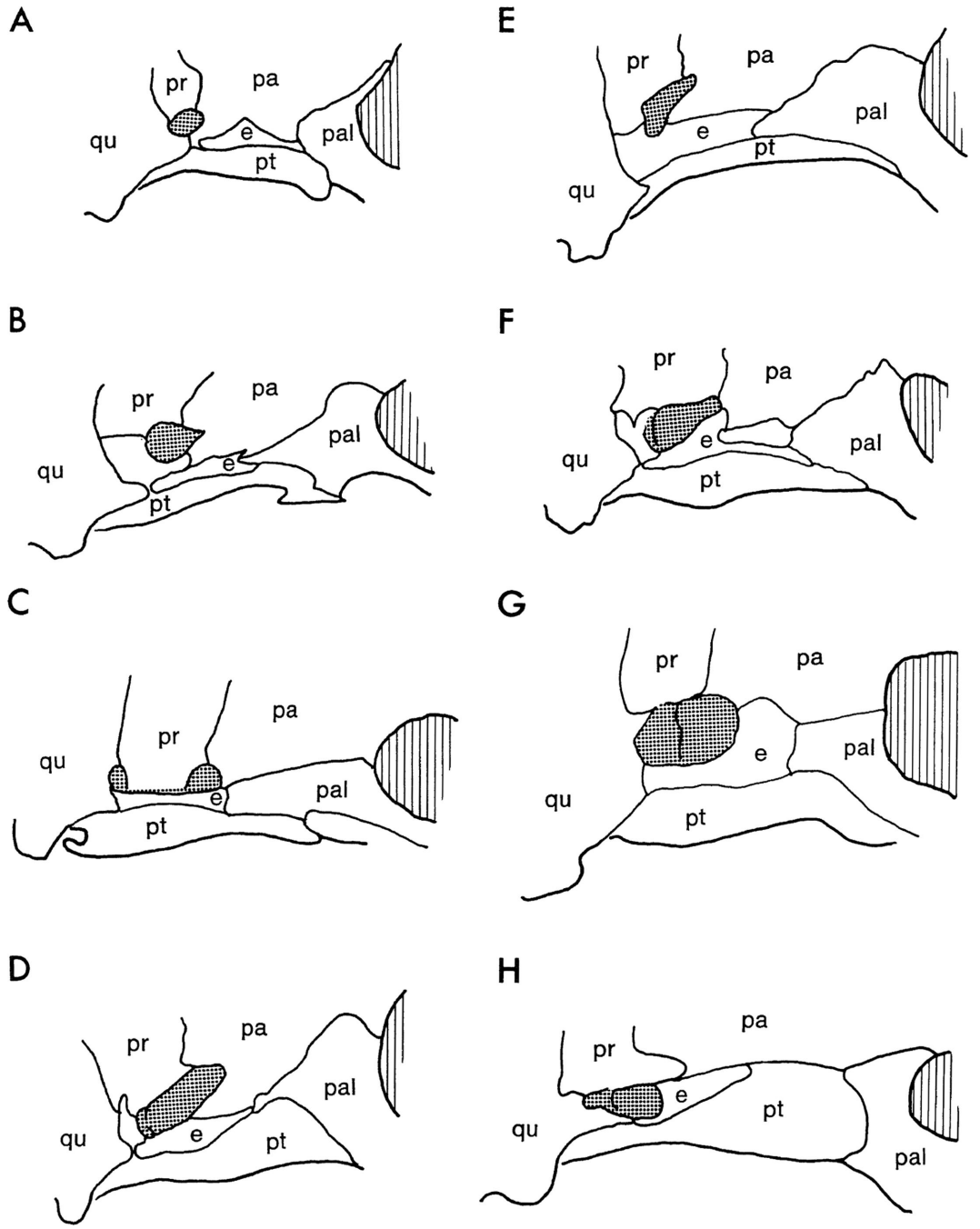

Fig. 13. The trigeminal region of eight trionychoid turtles showing contacts of the skull elements around the foramen nervi trigemini and participation by the palatine in the lateral wall of the braincase. The foramen interorbitale is crosshatched; the foramen nervi trigemini is stippled. Abbreviations: **e,** epipterygoid; **pal,** palatine; **pa,** parietal; **pr,** prootic; **pt,** pterygoid; **qu,** quadrate. **A.** *Dermatemys mawii* (BMNH 1911.1.28.1); **B.** *Staurotypus salvinii* (BMNH 1879.1.7.5); **C.** *Carettochelys insculpta* (BMNH 1903.4.10.1); **D.** *Lissemys punctata* (UF 56017); **E.** *Cyclanorbis elegans* (BMNH 1954.1.14.3); **F.** *Trionyx hurum* (BMNH 86.8.16.2); **G.** *Trionyx triunguis* (BMNH 62.3.20.8); **H.** *Chitra indica* (IRSNB 3295).

completely surround the columella (Gaffney, 1979b). Among cryptodires this occurs in the Trionychidae, *Carettochelys,* Chelydridae, and most Testudinidae (tables 10, 12).

Trigeminal Region

The trigeminal foramen lies lateral to the braincase and ventral to the processus trochlearis oticum of cryptodires (figs. 12, 13). In trionychids it is a large opening providing an exit for the maxillary and mandibular branches of the trigeminal nerve as well as the mandibular artery (Gaffney, 1979b). In trionychids the parietal, prootic, quadrate, pterygoid, and epipterygoid may contact this foramen but there is significant inter- and intraspecific variation in the degree and form of contact of each element (fig. 13).

An epipterygoid is present in all trionychid species but tends to fuse to the pterygoid in larger individuals (table 15). Fusion occurs less frequently (perhaps later in life) in trionychines than in cyclanorbines. Variation in the length of retention of a distinct epipterygoid is treated via three states of character 73 (tables 10, 11). This element usually fuses to the pterygoid in older adults of most cryptodires. Long-term retention of the epipterygoid is therefore considered to be a derived feature.

TABLE 15
Fusion of the Epipterygoid to the Pterygoid in Trionychid Turtles[a]

Species	N	A	B	C
aubryi	7	94.5	88.0	122.0
bibroni	7	119.0	119.0	119.0
cartilagineus	7	131.5	none	131.5
elegans	5	125.0	122.0	130.0
euphraticus	9	83.3	none	83.3
ferox	9	110.0	none	110.0
formosus	4	79.0	none	79.0
frenatum	4	107.3	134.0	134.0
gangeticus	7	110.0	111.0	111.0
hurum	4	99.0	none	99.0
indica	8	195.0	none	195.0
leithii	3	108.0	none	108.0
muticus	3	39.5	41.5	41.5
nigricans	1	105.0	none	105.0
punctata	6	50.0	38.0	81.5
senegalensis	6	80.3	75.0	117.5
sinensis	9	58.5	none	58.5
spiniferus	8	59.5	none	59.5
steindachneri	1	43.8	none	43.8
subplanus	4	61.6	104.5	104.5
swinhoei	1	67.0	none	67.0
triunguis	10	153.0	143.5	153.0

[a] Condylar length (in mm) of the largest skull with a free epipterygoid (A), the smallest skull with a fused epipterygoid (B), and largest skull measured (C) are given for each species.

Because the epipterygoid is an important landmark in describing variation in the morphology of the trigeminal region of trionychids, descriptions of this region are based on individuals in which this element is not yet fused to the pterygoid. The contacts described are those visible on the outside of the skull (as seen in fig. 13); in some cases internal contacts will differ. Complication of these descriptions arises because the epipterygoid is a superficial element of variable shape and size that can cover certain contacts in some individuals of a given species but not in others. This results in the ungainly appearance of the three states of character 70 (table 10) in which all states include the possibility of no pterygoid-trigeminal contact (the case when the epipterygoid is large), but show different forms of pterygoid-trigeminal contact if the epipterygoid is not enlarged. When the pterygoid does contact the foramen nervi trigemini the contact may occur posteriorly between the prootic and epipterygoid (state 1) (fig. 13B, D, F), ventrally between the epipterygoid and quadrate (state 0), anteriorly between the parietal and epipterygoid (state 2), or in no individuals at all (character 69, state 2) (fig. 13E, G). See table 11 for distribution of these character states.

Contact of the pterygoid to the foramen nervi trigemini between the prootic and epipterygoid (state 1, character 70) occurs in *Trionyx formosus, T. gangeticus, T. hurum, T. nigricans,* and *Lissemys punctata* and results in the isolation of the quadrate from the foramen nervi trigemini (fig. 13D, F). In both *Cyclanorbis* species and both *Cycloderma* species the quadrate is also isolated from the foramen nervi trigemini. But in this case it is the epipterygoid that meets the prootic posteriorly and thus intervenes (character 71, state 2; fig. 13E). When the epipterygoid fuses to the pterygoid, the two groups mentioned above (those with state 1 of character 70 and

those with state 2 of character 71) look identical.

Significant variation in this region among the outgroups makes assigning polarities to characters of contact of the epipterygoid to the foramen nervi trigemini difficult. Identification of polarity for other contacts in the trigeminal region seems clear. In no other trionychoid does the epipterygoid contact the prootic posteriorly (fig. 13A, B, D) as it does in *Cyclanorbis* and *Cycloderma* (character 71, table 11; fig. 13E) or anteriorly as it does in some or all members of certain trionychine species (character 71, table 11; fig. 13H). Similarly, all trionychoid outgroups have contact between the epipterygoid and palatine (fig. 13A–C) and the absence of this contact in some or all members of a species is considered derived (character 68, tables 10, 11).

An important feature of the Trionychoidea (sensu Gaffney, 1979b) is participation of the palatine in the formation of the lateral wall of the braincase. This occurs in all trionychoids examined and can be seen just anterior to the foramen nervi trigemeni (fig. 13). In trionychoids the pterygoid is excluded from the interorbital fenestra by the expanded palatines. In testudinoids and in other turtles the pterygoid either reaches the interorbital fenestra or is immediately adjacent to it (character 43, table 12) (fig. 12).

Occipital Region

There are numerous systematically useful characters visible on the skull in posterior view. One of these is a reflection of the importance of the internal carotid artery (Albrecht, 1967; McDowell, 1961; Gaffney, 1975, 1979b). The large diameter of the canalis carotici interni and the straight path that it follows in trionychoids can be observed even in articulated skulls. A stiff wire, slightly narrower than the canal, will pass into the foramen posterius canalis carotici interni and out of the foramen anterius canalis carotici interni with ease (character 57, table 12). In large trionychids the latter opening is clearly visible through the former. This is in contrast to the case in other cryptodires in which this canal makes an S-shaped curve or a high-angle bend (see figs. 25–29 in Gaffney, 1979b). It seems likely that this straight, wide path facilitates blood flow through the internal carotid in trionychoids.

The location of the foramen posterius canalis carotici interni in the Trionychidae is also of some interest. In all species of this family it is completely surrounded by the pterygoid (figs. 14D–F, 15A, C). The same is true for *Carettochelys,* but in kinosternids it can be open dorsally to the fenestra postotica (*Staurotypus*) or be bordered dorsally by the prootic (*Kinosternon* and *Sternotherus,* fig. 14C). In *Dermatemys* and in most testudinoids and chelydrids it is open dorsally to the fenestra postotica (character 56, table 12; fig. 14A, B).

In some trionychids the foramen posterius canalis carotici interni is quite ventrally located and is reminiscent of the condition in the "Paracryptodira" (fig. 15C). However, in all other trionychoids and other Eucryptodira it is posteriorly located. Thus the presence of these foramina on the ventral surface of the skull is considered derived.

Variation in the location of the foramen posterius canalis carotici interni within the Trionychidae is best described in relation to a crest of bone which is a lateral extension of the tuberculum basioccipitale. In no member of this family is this foramen located above such a crest, but in *Pelochelys bibroni, Chitra indica, Trionyx cartilagineus,* and *T. nigricans* (only one specimen available) it is found within the crest (see fig. 15; foramen posterior canalis carotici interni is visible in A and C but not in B). The latter condition is considered to be primitive relative to the ventral position found in all other species (character 60, table 11).

The foramen jugularis posterius is located lateral to the foramen magnum in turtles and is visible in posterior view. In most cryptodires it is surrounded by the exoccipital or exoccipital and opisthotic (fig. 14A–C). In some cheloniids, some trionychids, and some *Claudius* and *Platysternon,* this opening is continuous with the fenestra postotica (fig. 14D). Isolation of the foramen jugularis posterius from the fenestra postotica when present in the Trionychidae occurs in a unique manner: that is, by contact of the pterygoid to the opisthotic (fig. 14E, F). In all cyclanorbines the pterygoid arches dorsally to meet the opisthotic (fig. 14F). In the trionychines, infrequent isolation occurs via the descent of

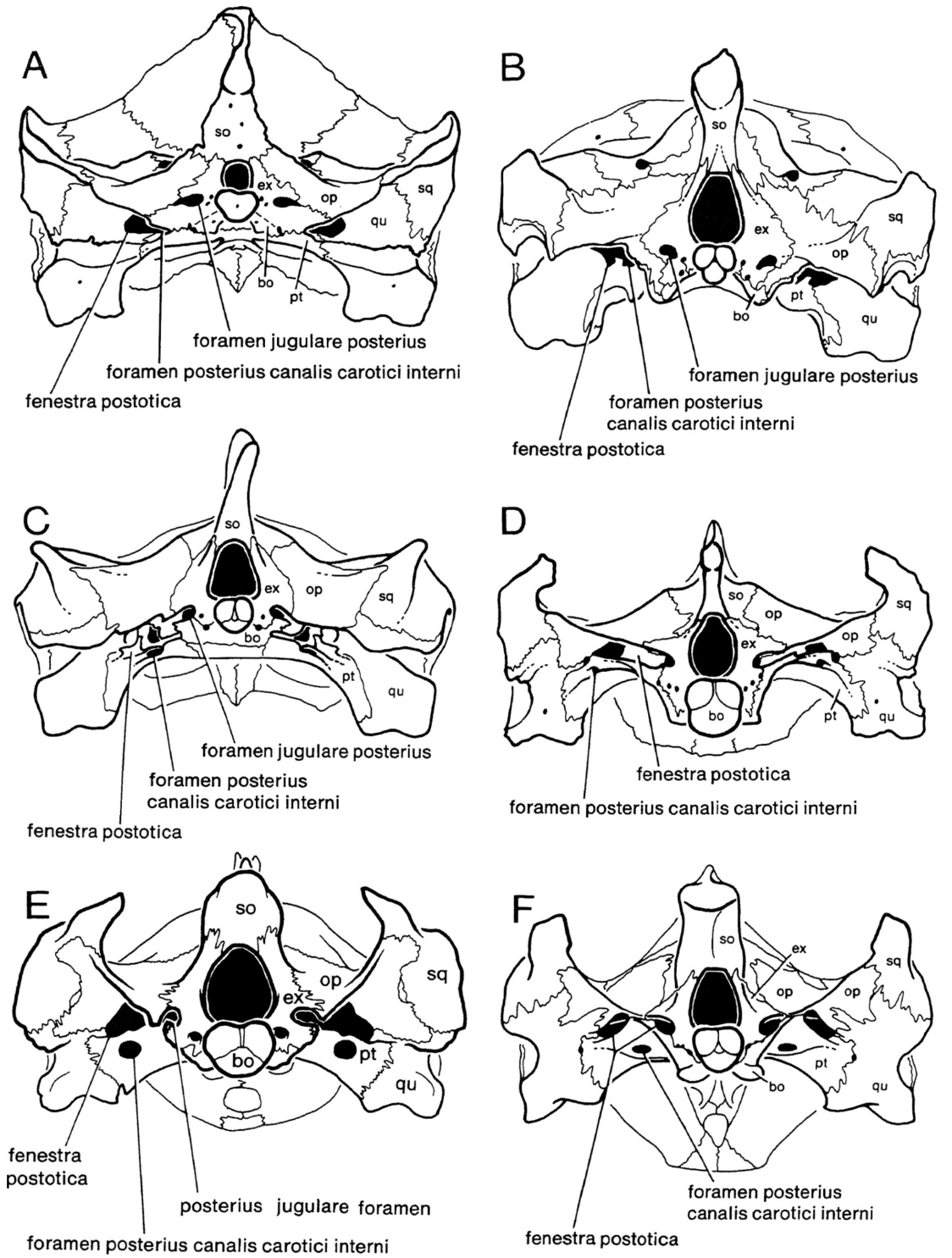

Fig. 14. Posterior views of the skull of six eucryptodiran turtles. **A.** *Macroclemys temminckii* (AMNH 58251); **B.** *Chinemys reevesi* (AMNH 31117); **C.** *Sternotherus odoratus* (AMNH 69752); **D.** *Pelochelys bibroni* (AMNH 23541); **E.** *Pelodiscus sinensis* (UF H 2406); **F.** *Lissemys punctata* (NMNH 61094).

a narrow process of the opisthotic across an otherwise open fenestra postotica (fig. 14E). These two types of isolation of the foramen jugulare posterius appear to be independent evolutionary events (Loveridge and Williams, 1957) and are treated as such in the analysis of intrafamilial relationship (characters 58 and 59, table 11).

In nearly all trionychids, as in most other trionychoids and in chelydrids (including *Platysternon*) and chelonioids, there is contact between the exoccipital and pterygoid. Only in *Trionyx triunguis* does the basioccipital intervene between these elements, separating them as it does in most testudinoids. In the current context this is a unique feature most useful for the recognition of *T. triunguis* (character 63, table 13). Separation of the pterygoid from the exoccipital may be a shared derived feature of the Testudinoidea.

The basis tuberculi basalis is a small tubercle on the dorsal surface of the basioccipital found within the braincase. When present this tubercle is visible (under correct lighting) through the foramen magnum. Gaffney (1979b) reported that it is variably developed in most turtles but that it is missing in *Trionyx ferox*. I find this structure to be absent in all trionychoids and testudinids examined, but clearly visible in cheloniids, dermochelyids, chelydrids, and emydids (but not *Rhinoclemmys pulcherrima*). This is therefore a useful character at the interfamilial level (character 55, table 12).

Palate

The most striking differences between the palates of trionychids and those of other cryptodires is the presence of a median foramen anterior to the apertura narium internum and the presence of unconstricted pterygoids (fig. 15). This midline opening is usually of large size and is called the foramen intermaxillaris. It varies in size in the Trionychidae (see below, character 74) but it always separates the vomer from the fused premaxillae. The same structure appears to be present in *Carettochelys* where it is continuous with the apertura narium internum. In *Carettochelys* the vomer and maxillae do not meet anterior to the apertura narium internum and the posterior limits of the foramen intermaxillaris remain undefined.

A structure that appears to be homologous to the foramen intermaxillaris is present in mature individuals of all three living staurotypine kinosternids and in *Xenochelys formosus* (Oligocene of South Dakota, Williams, 1952). The deep pit in the premaxillae, which accommodates the symphyseal projection of the lower jaw in all kinosternids, opens dorsally in large individuals of both species of *Staurotypus*, in *Claudius*, and in *Xenochelys*. This does not occur in large individuals of any other living turtles with strongly hooked lower jaws such as chelydrids (including *Platysternon*). In staurotypines, this opening accommodates the sharply hooked symphysis of the lower jaws as it does in *Carettochelys*. Trionychids always have the foramen intermaxillaris in spite of the fact that they have unhooked lower jaws (character 47, table 12).

Variation in the size of the foramen intermaxillaris among trionychids has been utilized by several authors (Loveridge and Williams, 1957; De Broin, 1977). Comparison of the length of the foramen intermaxillaris relative to the total skull length is not satisfactory; the distribution of this character for trionychids is quite continuous (fig. 2). It should be noted, however, that the members of a proposed monophyletic group (Meylan, 1985), the North American forms plus *Trionyx swinhoei, T. euphraticus,* and *T. triunguis,* have the highest values for the ratio of foramen intermaxillaris length to total skull length.

This character can be utilized if examined in terms of foramen size relative to the primary palate. Variation in the ratio of length of the foramen intermaxillaris to length of the primary palate among trionychids falls into five distinct groups (fig. 2, table 10). Identification of a character polarity for the states of this character is difficult. The foramen intermaxillaris in other trionychoids is highly specialized in one case (*Carettochelys*) and incompletely developed in the other (Staurotypinae). It appears prudent to assume that the medium size classes together approximate the primitive state and that the most divergent conditions (states 0 and 2) are

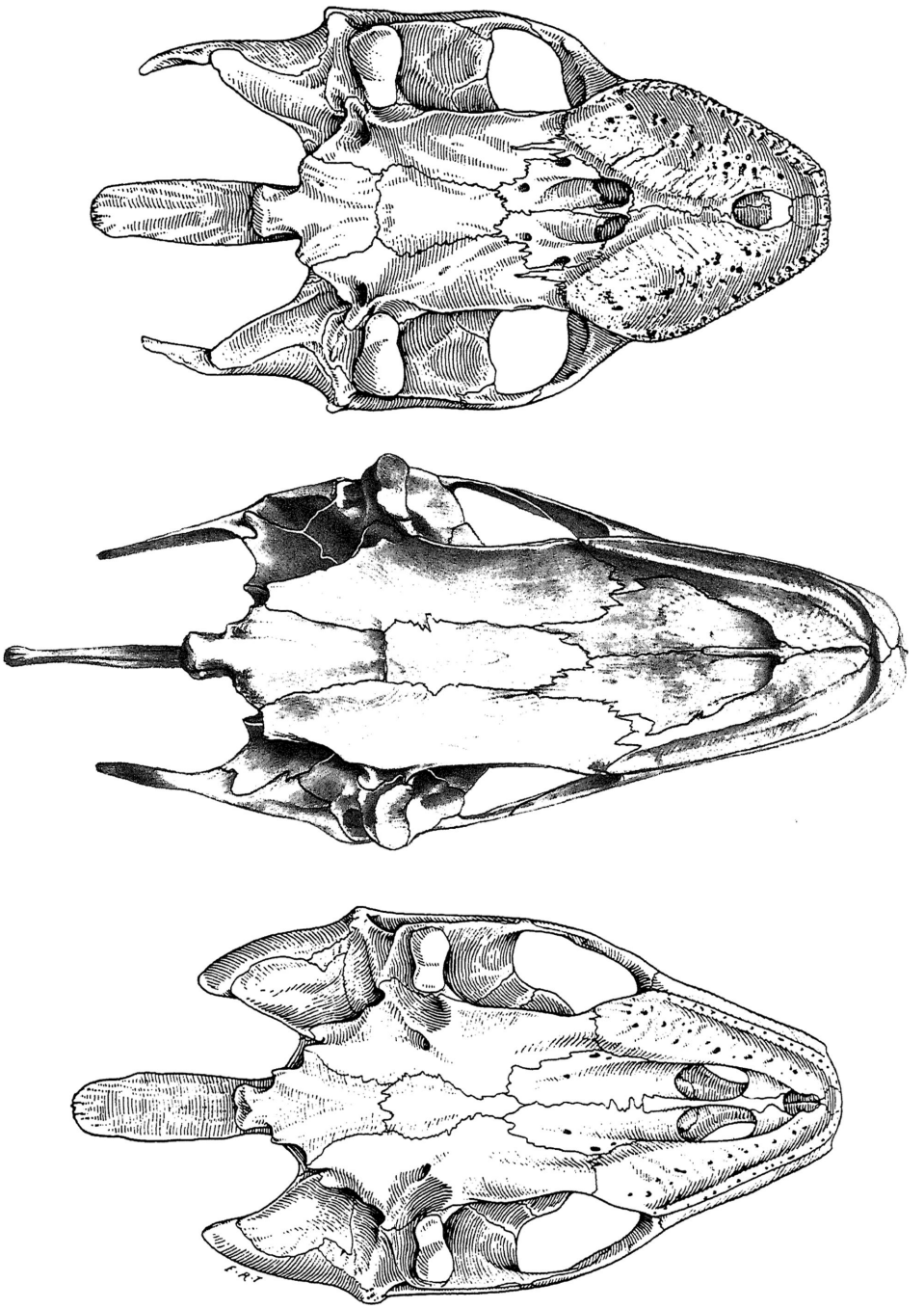

Fig. 15. Ventral view of the skulls of three trionychid turtles. **Top,** *Trionyx triunguis* (BMNH 1947.3.6.12, modified from Loveridge and Williams, 1957); **middle,** *Chitra indica* (from Gray, 1855, presumably BMNH specimen, sutures added from MCZ 29487); **bottom,** *Cyclanorbis senegalensis* (BMNH 65.5.9.20, from Loveridge and Williams, 1957).

derived within the Trionychidae (character 74, tables 11, 13).

The vomer is one of several elements which is reduced in the Trionychidae. In most turtles it lies between the paired maxillae and palatines. Anteriorly it reaches the premaxillae and posteriorly it often contacts the paired pterygoids. When a foramen intermaxillaris is present, premaxillary contact is prevented. In some trionychids the vomer divides the maxillae completely and reaches the foramen intermaxillaris between them (fig. 15C). This most closely approximates the condition in the outgroups in which no foramen intermaxillaris is present and is therefore considered to be the primitive condition for the relationship of the vomer to the maxillae (character 48, table 11).

In other trionychids the maxillae meet on the midline of the palate ventral to the vomer. Depending on the degree of reduction of the vomer and the length of this intermaxillary suture, the vomer may still enter the foramen intermaxillaris by reaching it dorsally over the united maxillae. Reduction of the vomer to the extent that it does not reach anteriorly to the foramen intermaxillaris is interpreted as the derived state of character 49 (table 11).

Posteriorly, the vomer of most cryptodires reaches between the paired palatines as far as the pterygoids. This is true of *Dermatemys* and kinosternids, but not *Carettochelys* or any trionychids (fig. 15). The failure of the vomer to reach as far posterior as the pterygoids is considered a derived condition (character 50, table 12).

In most chelonians the vomer is the only unpaired midline element reaching the transverse pterygoid-palatine suture. In *Carettochelys* and all trionychids (except *T. euphraticus*), only an enlarged basisphenoid does so (fig. 15). This unique contact of palatal elements has been recognized as evidence of unique common ancestry of these two taxa (Baur 1891b; Meylan, 1985). It is treated as such here (character 46, table 12). The absence of contact of palatines and basisphenoid in most specimens of *T. euphraticus* appears to be a unique reversal (character 46, table 13).

The vomer of turtles does not normally contact the basisphenoid, but with the anterior extension of the latter in trionychids comes a greater possibility that such contact might occur. Siebenrock (1897) reports vomer-basisphenoid contact on the dorsal surface of the palate in *Pelochelys*. In two of the seven *Pelochelys* skulls examined during this study (USNM 231523 and NMW 1857), contact between these elements is present on the palate. This condition is unique to *Pelochelys* among the Trionychidae (character 51, table 13). In *Cycloderma frenatum* the vomer is absent. This is a unique condition among trionychids (character 66, table 13).

At or near the palatine-pterygoid suture in all chelonians is located a paired ventral opening in the palate, the foramen palatinum posterius. This opening is never large in trionychids (fig. 15). It may be entire, divided into two openings, or divided into numerous small openings not larger than the nutritive foramina of the palate. Small size of these openings may be a feature shared by all trionychoids as well as some testudinoids, but the variation in the division of this opening is useful within the Trionychidae, and in particular among the Cyclanorbinae (character 53, table 11). Division of the foramen palatinum posterius is considered derived.

The contacts of the foramen palatinum posterius also vary among the living species of the Trionychidae. In most trionychids, as in most chelonians, these foramina contact the palatine and the pterygoid and/or maxillary. In a limited number of trionychids this opening is restricted to the palatine, which is considered to be a derived condition (character 54, table 11).

The processus pterygoideus externus of cryptodires usually takes the form of a moderate to short posterior or posterolateral projection from the anterolateral edge of the pterygoid just anterior to some degree of medial constriction. It is found in nearly all cryptodires and varies considerably in degree of development. In trionychids there is no medial constriction of the pterygoids and no free projection of this process (fig. 15). In *Carettochelys*, the pterygoids are only slightly constricted and the processus pterygoideus externus projects very weakly or not at all. In other trionychoids these processes may be present (*Kinosternon, Staurotypus,* some *Dermatemys,* some *Claudius*) or absent (some

Claudius, some *Dermatemys, Xenochelys*), but they are never as large and posteriorly projecting as in the Chelydridae or some of the Emydidae. Reduction of this projecting quality could be a shared derived feature of the Trionychoidea. It occurs elsewhere among the Cheloniidae (*Chelonia*), "Bataguridae" (*Malayemys*), and Testudinidae (several genera). The absence of a projecting processus is certainly derived for the Trionychidae and possibly for the Trionychidae plus *Carettochelys* (character 52, table 12).

The elongate basisphenoid of trionychids varies in shape. In most species, as in the outgroups, it has a subtriangular shape although it is usually somewhat more elongate. In a few forms medial constriction of the basisphenoid occurs either occasionally or frequently. The presence of an hourglass shaped basisphenoid is considered derived within the Trionychidae (character 64, table 11).

VARIATION IN THE VISCERAL SKELETON AND NONSHELL POSTCRANIA

Although the nonshell postcranial elements of turtles have been shown to provide valuable systematic data and are important in currently used arrangements, they have not been used extensively. The most important modern studies of the systematic value of nonshell postcrania are found in Williams (1950) and Zug (1971). Williams' (1950) monograph on the cervical articulations of turtles forms the foundation of the most frequently used modern classifications of turtles (see discussion). Zug (1971) provided data on the pelvic girdle and hind limbs which has since been cited as evidence for the recent realignment of certain cryptodires (Gaffney, 1975, 1984).

In the current attempt to determine the best hypothesis of relationships for trionychids, data from the cervical and thoracic vertebrae, the hyoid, and the pelvic and pectoral girdles have been found to be extremely valuable. Characters of the appendages and caudal vertebrae are of less use. The visceral skeleton has been included with the other nonshell postcrania in an effort to balance the size of the three osteological data sets.

With the exception of the hyoid and the lower jaw, the characters treated in this section are most valuable in determining interfamilial relationships of trionychids. The hyoid and lower jaw are also important at this level but prove to be of additional value in the study of intrafamilial relationships.

MANDIBLE

The lower jaw of trionychids is remarkable for its very high coronoid processes and large retroarticular processes (Boulenger, 1889) and for the significant contribution to the area articularis mandibularis made by the surangular (compare figs. 16 and 17). The retroarticular process is much larger than that of other turtles (except *Carettochelys*) and adds 10 percent or more to the total length of the jaw (character 99, tables 16, 18).

As observed by Gaffney (1979b), the prearticular and surangular of trionychids are frequently in contact, restricting or subdividing the fossa meckelii (fig. 17, top). In 82 percent (81/98) of the trionychids examined the prearticular and surangular meet either on the posterior edge of the fossa meckelii (36/98) or divide it by meeting across the middle (45/98). There is no clear pattern of variation among the species within the family. All 3 conditions occur in three taxa; 2 of 3 conditions occur in 11 others. The high incidence of surangular-prearticular contact across the fossa meckelii could be considered a shared derived feature of the family Trionychidae. However, it occurs in several other taxa and absence of a clear distribution makes this character unusable. In *Carettochelys* one-half of the specimens (N = 4) examined show this contact. Elsewhere among cryptodires it occurs in some *Kinosternon,* in *Dermatemys,* in *Platysternon,* and in some pleurodires.

In most turtles the area articularis mandibularis is made up by the articular with little or no contribution from the surangular (fig. 16, top). Only in the Trionychidae and *Carettochelys* does the surangular make up one-half or more of this surface (fig. 17, top). The surangular is always included in this area in other trionychoids but always forms less than half of the articular surface. In testudinoids and chelydrids the surangular is frequently absent from the area articularis mandibularis and when present contributes less

TABLE 16
Systematic Characters and Character States of the Lower Jaw and Nonshell Postcrania of Trionychid Turtles

Characters	Character states
79. entepicondylar foramen open along humerus	1. no 2. variable 3. yes
80. hyperphalangy of manus digits 4 and 5, pes digit 4	1. no 2. yes
81. radius and ulna in contact adjacent to manus	1. no 2. yes
82. number of clawed digits of manus	1. 5 2. 3 or fewer 3. 2 or fewer
83. cervical centra 2–7 opisthocoelus	1. no 2. yes
84. centra of 8th cervical and 1st body vertebrae in contact	1. yes 2. no
85. ventral process on 8th cervical	1. present 2. absent
86. ventral process on 8th cervical	1. single 2. double
87. ventral keel on 8th cervical present and limited to posterior end	1. no 2. yes
88. strong dorsal processes on cervicals	1. no 2. yes
89. number of posterior body vertebrae with transverse processes not reaching pleurals	1. 0 2. 1 3. 2
90. number of ossifications in corpus hyoidis	1. 1 2. 6 3. 8
91. number of ossifications in cornu branchiale II	1. 1 only 2. 2–6 3. 7 or more
92. ossifications of cornu branchiale II broad and strongly sutured	1. no 2. yes
93. basihyals in close contact and projecting anteriorly	1. no 2. yes
94. surangular forms part of area articularis mandibularis	1. less than ½ to 0 2. less than ½ 3. greater than or equal to ½
95. symphyseal ridge strong and present in a depression	1. no 2. yes
96. foramen nervi auriculotemporalis with two lateral openings	1. no 2. yes
97. foramen nervi auriculotemporalis with one lateral and one dorsal opening	1. no 2. yes
98. foramen intermandibularis caudalis enclosed by prearticular	1. sometimes 2. never
99. retroarticular process large, about one-tenth of total lower jaw	1. no 2. yes
100. ilia curve medially	1. no 2. yes
101. ilia curve posteriorly	1. no 2. yes
102. ilia anteroposteriorly expanded at distal end	1. yes 2. no
103. thelial process present	1. no 2. yes
104. pubis and ischium closely opposed or in contact across thyroid fenestra	1. no 2. yes
105. epipubic region ossifies	1. yes 2. no
106. pectineal processes and interpubic suture lie in a single plane	1. no 2. yes
107. ischia extend into thyroid fenestra	1. yes 2. no
108. pectineal processes equal to or wider than interpubic contact	1. no 2. yes
109. metischial processes present and distinct	1. yes 2. no
110. ilioischial notch	1. absent 2. present
111. coracoid shortest of three pectoral processes	1. no 2. yes
112. angle of acromion process to scapula approaches that of coracoid to acromion	1. no 2. yes
113. coracoid longest of three pectoral processes	1. no 2. yes

than half the articular area. The large contribution by the surangular in trionychids must be considered derived. The condition in other trionychoids appears to be intermediate between the state in the Trionychidae and that in other turtles (character 94, table 18).

An important systematic character in the lower jaw of trionychids is the presence of a

TABLE 17
States for Characters Found to be Useful in Hypothesizing Relationships Among Recent Trionychid Turtles[a]

Species	Characters												
	95	98	100	107	109	87	88	112	113	90	91	92	93
aubryi	1	2	2	1	2	1	2	1	1	2	1	1	2
bibroni	1	1	1	2	1	2	2	2	2	3	2	2	1
cartilagineus	2	1	1	2	1	2	1	1	2	3	2	1	1
elegans	1	2	1	2	2	1	1	2	1	2	1	1	2
euphraticus	1	2	1	2	2	2	1	1	2	3	3	1	1
ferox	1	1	1	2	2	1	1	1	2	3	3	1	1
formosus	2	2	1	2	—	—	—	—	—	—	2	1	1
frenatum	1	2	2	1	2	1	2	1	1	2	1	1	2
gangeticus	2	1	1	2	1	1	1	1	2	2	3	1	1
hurum	2	1	1	2	1	1	1	1	2	3	1	1	1
indica	1	2	1	2	1	2	2	2	2	3	2	2	1
leithii	2	1	1	2	1	1	1	1	2	2	2	1	1
muticus	1	1	1	2	1	1	1	2	2	2	2	1	1
nigricans	2	1	1	2	1	1	1	1	2	2	2	1	1
punctata	1	2	1	1	2	1	1	1	2	2	1	1	2
senegalensis	1	2	2	2	2	1	1	2	1	2	1	1	2
sinensis	1	1	1	2	1	1	1	1	2	2	2	1	1
spiniferus	1	1	1	2	1	1	1	2	2	2	3	1	1
steindachneri	1	1	—	2	—	—	—	—	—	2	2	1	1
subplanus	2	1	1	2	1	1	1	1	2	3	2	1	1
swinhoei	1	2	—	2	—	—	—	—	—	3	—	1	1
triunguis	1	1	1	2	1	1	1	1	2	2	2	1	1

[a] See table 16 for explanation of characters and character states.

sagittal ridge on the triturating surface at the symphysis (De Broin, 1977). This ridge usually forms within a depression on an otherwise flat surface (fig. 17, top). Such a single ridge does not occur in other turtles and appears to be derived within the Trionychidae. Among the members of this family a ridge occurs only in the Indian species, and in *Trionyx cartilagineus* and *T. formosus* (character 95, table 17). A ridge is also present in the largest individuals of *T. subplanus*.

The foramen nervi auriculotemporalis is a single or multiple opening in the surangular ventral to the area articularis mandibularis. Gaffney (1979b) reported multiple openings for this foramen only in *Podocnemis expansa*. Two or more lateral openings are also present in some specimens of almost every species of trionychid. Additional pleurodires (*Pelusios castaneus*) and also some testudinoids (*Cuora, Graptemys,* and *Geoclemys*) also have multiple lateral openings in the surangular. The occurrence of multiple lateral openings in the surangular, representing a divided foramen nervi auriculotemporalis, is considered derived (character 96, table 18).

Gaffney (1979b) mentioned an additional, apparently unnamed, foramen in the surangular that communicates with the foramen nervi auriculotemporalis and the fossa meckelii. Unlike the foramen nervi auriculotemporalis, it opens dorsally, not laterally. It is mentioned as occurring in *Staurotypus* and *Terrapene*. I have noted this opening in all kinosternids examined, and in *Platysternon*, but in no other taxa. The occurrence of the opening can clearly be considered derived and it appears to be a shared derived character for the Kinosternidae (character 97, table 18).

On the lingual surface of the jaw, in the suture between the prearticular and the angular, there may appear two foramina, the foramina intermandibularis oralis and caudalis (fig. 16, bottom). In most turtles there is evidence of both. In trionychids the anterior one (oralis) is never present and the pos-

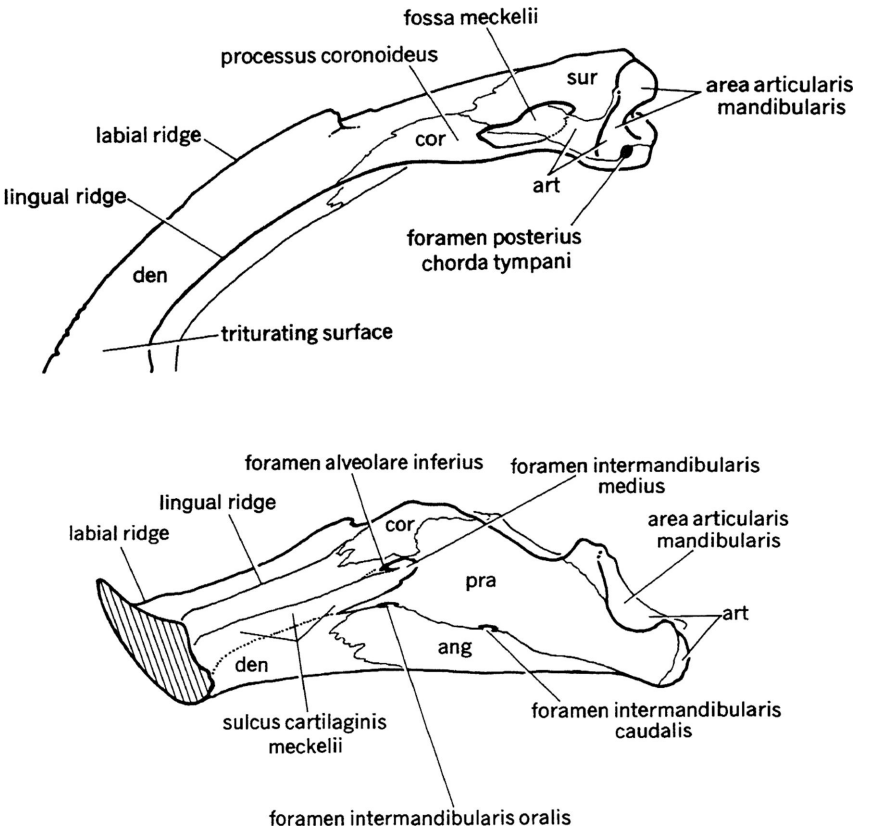

Fig. 16. Lower jaw of *Chelydra serpentina* (AMNH 67015). **Top,** dorsal view of right ramus; **bottom,** medial view of right ramus. Abbreviations: **ang,** angular; **art,** articular; **cor,** coronoid; **den,** dentary; **pra,** prearticular; **sur,** surangular. Symphysis is crosshatched.

terior one (caudalis) may be present or absent in some species, but is always absent in others (character 98, table 17). This uniform absence of the foramen intermandibularis caudalis is considered to be derived within the Trionychidae.

Hyoid

The hyoid of most cryptodires is not an elaborate structure. It typically consists of a single basal unit, the corpus hyoidis, which may or may not be ossified, and two pairs of branchial horns, cornu branchiale I and II, the anterior pair of which is always ossified (fig. 18A). By contrast, the hyoid of trionychids always consists of a minimum of ten ossifications and may include as many as 40 (fig. 18B–F). The corpus hyoidis is composed of either three pairs of ossifications (one pair of basihyals and two pairs of basibranchials, fig. 18B, E), or four pairs of ossifications (an additional pair is present anterior to the basihyals, fig. 18C, D, F). Cornu branchiale I always consists of a single ossification while cornu branchiale II consists of 1 to 18 ossifications.

Ossification of the corpus hyoidis from numerous centers has been recognized as a unique feature of the Trionychidae (Siebenrock, 1913; Romer, 1956) (character 90, table 18). This highly developed structure is also known to vary among the species of the Trionychidae (Annandale, 1912; Siebenrock, 1913), and characters of the hyoid appear to be useful in assessing intrafamilial relationships.

Most members of the Trionychidae have

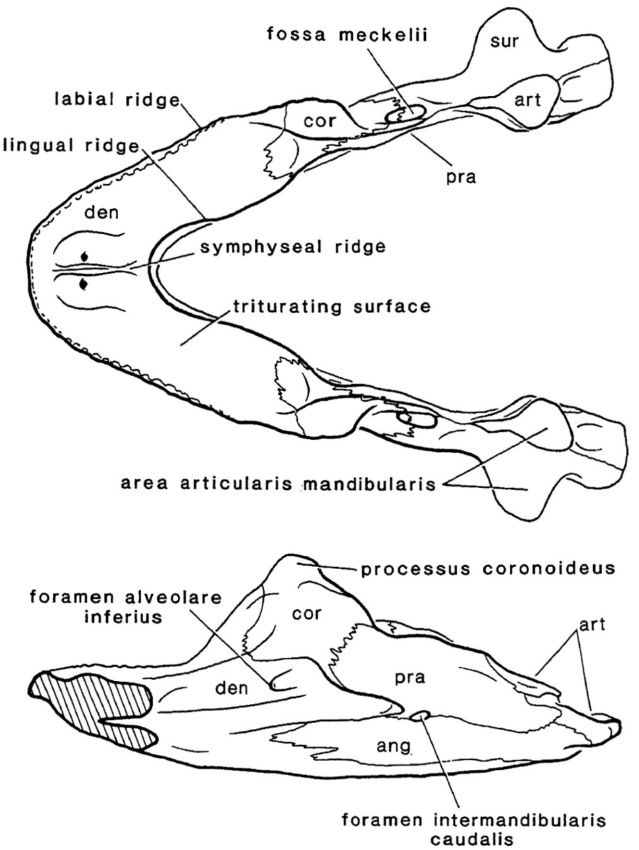

Fig. 17. Lower jaw of *Trionyx cartilagineus* (RH 129). **Top,** dorsal view, **bottom,** medial view of right ramus. Abbreviations are same as for figure 16.

six ossifications of the corpus hyoidis throughout life. However, in eight species the corpus has six ossifications in subadults but a total of eight ossifications at full maturity (character 90, table 17). This exceptionally high number in these select species is considered to be a further derived state.

Cornu branchiale I is a single ossification in all adult cryptodires examined in the course of this study. Cornu branchiale II, when ossified, also consists of a single element, except in some trionychids. In all of the Cyclanorbinae (fig. 18B) and in most *Trionyx hurum* (fig. 18C) it ossifies from a single center. In the remainder, it ossifies from as few as 2 to as many as 18 centers. Interspecific variability in the number of centers of ossification in cornu branchiale II falls into two seemingly natural groups with two exceptions. In most Old World forms the second horn includes six or fewer ossifications (fig. 18C–E). Only among living New World species and *T. euphraticus* does it always consist of seven or more (fig. 18F; character 91, table 17). In *T. gangeticus* it consists of 5 to 14 centers ($\bar{x}$ = 8.4) and in *T. sinensis* it consists of 3 to 9 centers ($\bar{x}$ = 5.1). These two species are assigned to a group based on their average number of ossifications. As is the case for the corpus hyoidis, a high number of ossifications in cornu branchiale II is considered derived.

In *Chitra indica* and *Pelochelys bibroni,* cornu branchiale II consists of three ossifications which are very broad and strongly sutured to one another (fig. 18D). This is a unique condition within the Trionychidae (character 92, table 17).

The corpus hyoidis of cyclanorbine trionychids can always be recognized by the close

TABLE 18
Distribution of the States of Characters of the Mandible and Nonshell Postcrania Used to Develop a Hypothesis of Relationship of the Trionychidae to Other Turtles[a]

Taxa	Characters																											
	79	80	81	82	83	84	85	86	89	90	94	96	97	99	100	101	102	103	104	105	106	107	108	109	110	111	113
Trionychidae	3	2	2	2	2	2	2	—	2	2 or 3	3	2	1	2	*	2	2	1	1	2	2	*	2	*	1	1	*
Carettochelys	1	1	2	3	2	1	1	2	2	1	3	1	1	2	2	1	1	2	1	2	1	2	1	1	1	1	2
Claudius	3	1	1	1	1	1	1	2	3	1	2	1	2	1	2	1	1	2	1	1	2	1	1	2	2	1	1
Staurotypus	3	1	1	1	1	1	1	2	3	1	2	1	2	1	2	1	1	2	1	1	1	1	1	2	2	1	1
Kinosterninae	2	1	1	1	1	1	1	2	3	1	2	1	2	1	2	1	2	2	2	1	1	1	1	1	2	1	1
Dermatemys	2	1	1	1	1	1	1	1	2	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1
Chelydridae	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Platysternon	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1
Cheloniidae	3	1	2	3	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	2	2	1	1	2	1	1	2
Emydidae	2	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1	2	1	1	1	1	1	1	2	1
Testudinidae	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	2	1	1	1	1	1	2	1
Pleurodira	2	1	1	1	1	1	—	—	1	1	1	2	1	1	1	1	1	1	1	—	1	—	1	—	1	1	1

[a] See table 16 for explanation of characters and character states. Characters marked with an asterisk are variable (see table 17).

contact and anterior projection of the basihyal pair which is always the anteriormost of three pairs of ossified elements (fig. 18B). Projections of this kind do not occur in trionychines with six basal elements, or in the corresponding elements in those species with eight basal ossifications. Anterior projection of the bony corpus is therefore considered derived for the Cyclanorbinae (character 93, table 17).

Cervical and Body Vertebrae

As early as 1876 it was recognized that trionychids had unique cervical articulations (Vaillant, 1876) and the cervical series continues to be used as strong evidence for monophyly of the Trionychidae (Boulenger, 1889; Siebenrock, 1902; Loveridge and Williams, 1957) and for monophyly of the Trionychidae plus Carettochelyidae (Meylan, 1985). In both families all cervicals are opisthocoelous (character 83, table 18) except for the eighth in trionychids, which has no central contact to the first thoracic vertebra (character 84, table 18). All other cryptodires have at least one biconvex vertebra (number 2, 3, or 4), some procoelous vertebrae, and contact between the centrum of the first thoracic vertebra and the centrum of the eighth cervical (Williams, 1950).

The members of the Trionychidae are also unique in having no ventral process on the eighth cervical (fig. 19B). A single or double process is present on the eighth cervical of all other cryptodires (fig. 19A, C, D; character 85, table 18). Its absence in this family can be correlated with the unique neck-packing mechanism described by Dalrymple (1979). The double ventral process of the eighth cervical, which is found only in kinosternids and *Carettochelys* (fig. 19C, D), is considered to be derived but lost in trionychids (character 86, table 18).

The only relief on the ventral surface of the eighth cervical of trionychids is a small posterior keel found in a few large species (character 87, table 17). Such keels are absent in other trionychoids and are considered to be derived within the family.

Like other cryptodires, most trionychids lack dorsal processes of the cervicals. However, four species have very well developed

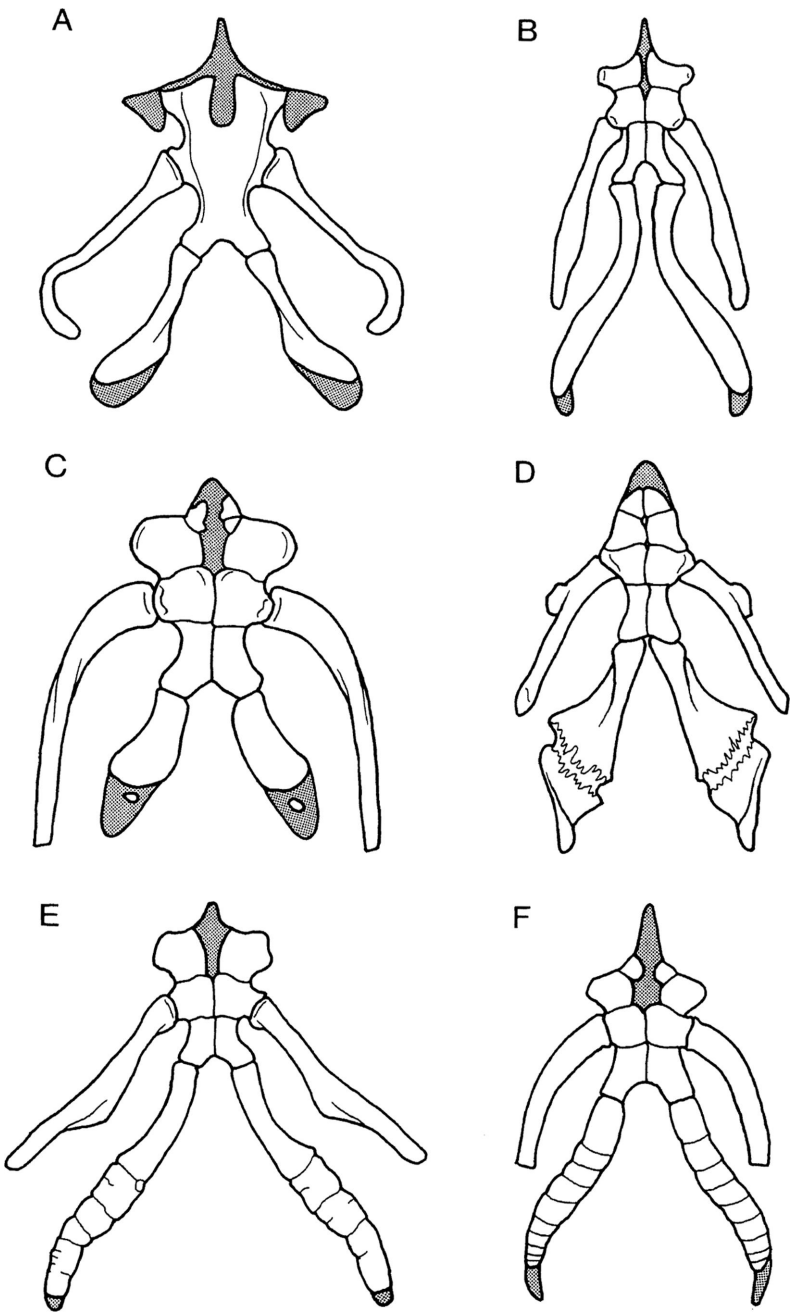

Fig. 18. Dorsal views of the hyoids of six eucryptodiran turtles. **A.** *Mauremys caspica* (after Siebenrock, 1913); **B.** *Lissemys punctata* (after Annandale, 1912); **C.** *Trionyx hurum* (modified from Annandale, 1912); **D.** *Chitra indica* (BMNH 1984.1276); **E.** *T. gangeticus* (after Annandale, 1912); **F.** *T. euphraticus* (after Siebenrock, 1913). Stippled areas represent unossified cartilage.

dorsal processes on the middle to posterior cervical vertebrae (fig. 20). The presence of these processes is considered derived (character 88, table 17).

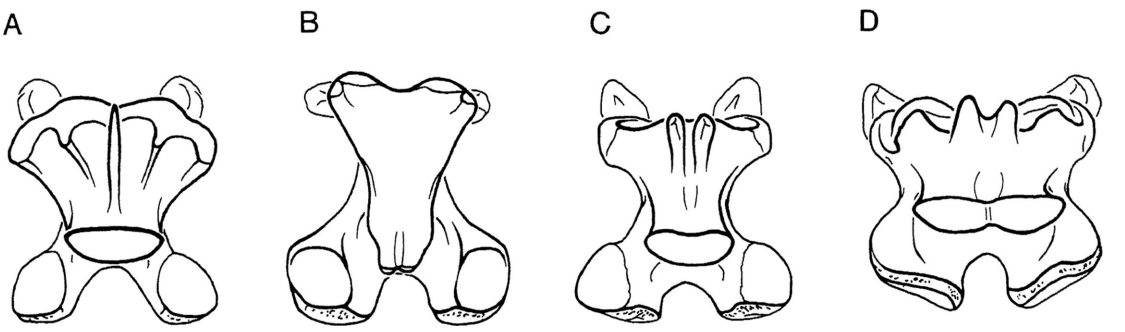

Fig. 19. Ventral view of the eighth cervical vertebra of four eucryptodiran turtles. **A.** *Trachemys scripta* (AMNH 111961); **B.** *Trionyx ferox* (AMNH 129737); **C.** *Staurotypus triporcatus* (83-JI-202); **D.** *Carettochelys insculpta* (UF 43823).

Chelonians have 10 thoracic vertebrae between the cervicals and the sacrals, and they normally have 8 pairs of pleural bones. Thus, two thoracic vertebrae are not associated with a pair of pleurals. One of these is the first body vertebra. It sends transverse processes posterolaterally to join the anterior edge of the ribs associated with the first pair of pleurals (fig. 6). The other vertebra which is without associated pleurals is the tenth. The tenth thoracic vertebra may be firmly fixed by transverse processes which brace it against a tuberosity on the eighth pleural (fig. 6A), or it may be somewhat less well fixed and have only remnants of transverse processes (fig. 6B, C; Zug, 1971). In the Kinosternidae the ninth thoracic vertebra is like the tenth in having no contact between the transverse processes and the carapace. In this family both the ninth and tenth vertebrae exhibit some freedom of movement.

The distribution among all turtles of these three conditions of the posterior thoracic vertebrae (character 89, table 18), suggests that reduced articulation between the shell and these posterior vertebrae is derived.

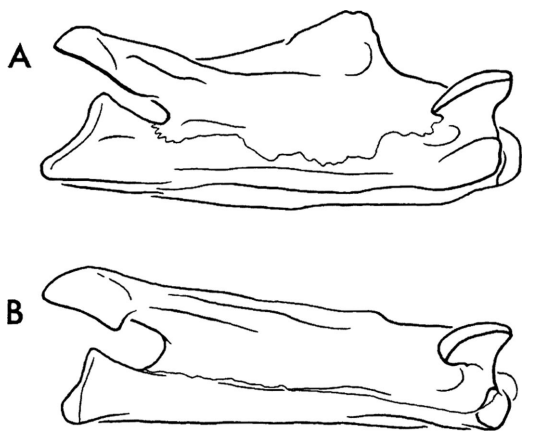

Fig. 20. Lateral views of the sixth cervical vertebrae of two trionychid turtles. **A.** *Cycloderma aubryi* (MRAC 19212); **B.** *Trionyx ferox* (AMNH 129737). Anterior is to the right.

Pelvis

Numerous features of the trionychid pelvic girdle are useful in phylogenetic analysis. There are no fewer than 10 characters which are germane to establishing interfamilial relationships. Three of these are used in the intrafamilial analysis as well. The pelvic girdle is treated as follows: ilium first, and then puboischiatic plate from anterior to posterior.

The ilia in most turtles extend dorsally from the acetabulum to meet the carapace and transverse processes of the sacral vertebrae. The main axis of the ilium is straight in all turtles except trionychids (Zug, 1971). In trionychids they are strongly flexed posteriorly (character 101, table 18). Zug (1971) indicated that these posteriorly curved ilia do not articulate with the carapace in trionychids. This is certainly the case in all trionychine trionychids, but carapacial contact does occur in some cyclanorbines (see discussion of shell character 21).

Hirayama (1985) has suggested that lateral

curvature of the ilia is a feature unique to the Testudinoidea. I believe he means medial curvature because I find medially curved ilia in all testudinoids examined. In numerous trionychoids including some trionychids (character 100, table 17), *Carettochelys, Dermatemys,* and most kinosternids (character 100, table 18) the ilia are also medially curved. The character state is therefore shared by all of Gaffney's (1984) Chelomacryptodira (Trionychoidea plus Testudinoidea). Its absence in most trionychids can be considered a loss of the condition, and thus derived within the family.

The dorsal end of the ilium of all turtles except trionychids and smaller kinosternines is anterioposteriorly expanded. This distal sagittal crest is the site where the transverse processes of the sacral vertebrae articulate. Based on a single individual, Zug (1971) described the distal end of the ilium of *Dermatemys* as being unexpanded. In four *Dermatemys* and in three *Carettochelys* (not examined by Zug) available for this study the distal ilia are anteroposteriorly expanded. The absence of this distal expansion is considered derived (character 102, table 18).

The thelial process, site of attachment for the iliotibialis muscle, has been considered to be a unique feature of the Kinosternidae (Zug, 1971). A topographically and morphologically similar structure occurs on the ilium of all three *Carettochelys* pelves available to me (fig. 21B, D). In addition, a small tubercle, in the position of the thelial process, is present in three of six individuals of *Lissemys punctata* examined (fig. 21E). The presence of a thelial process is considered to be derived for kinosternids and *Carettochelys* (character 103, table 18).

The epipubis is a small plate of cartilage or bone which extends anteriorly in a horizontal plane from the region of the pubic symphysis (fig. 21A, B). Hay (1908) has suggested that an unossified epipubis is primitive for turtles. Although it is the last center in the pelvic girdle to ossify it does ossify in all cryptodires except the most derived trionychoids (the Carettochelyidae and Trionychidae, fig. 21C–F), most cheloniids (Baur, 1891a, reports that some old cheloniids ossify the epipubis), and testudinids. The lack of ossification of the epipubis appears to be a derived and possibly paedomorphic feature (character 105, table 18).

The pectineal processes extend from the body of the pubis in an anterior or anterolateral direction. In most cryptodires they are small relative to the length of interpubic contacts (fig. 21A, B, D). The members of the Trionychidae are unique in having pectineal processes which are as wide as or wider than the length of interpubic contact (fig. 21C, E, F; character 108, table 18).

The pectineal processes and the interpubic symphysis of trionychids lie in a single plane and they all lie flat against the plastron (Zug, 1971). In nearly all other cryptodires no such common plane exists. The exceptions are living chelonioids and *Claudius,* but in these taxa the anterior pubic region does not lie flat on the plastron. In skeletons of very young specimens of *Kinosternon* and *Sternotherus* the entire pubis is quite flat. It appears that the pelvis first ossifies in a single plane and with age gains three-dimensional qualities. Thus the occurrence of a flat pubis in trionychids may be a retention of the juvenile state (charactor 106, table 18).

The thyroid fenestra is the major opening in the puboischiatic plate. In turtles it is often partially or completely divided by bone (fig. 21A). Bony division occurs in two nonhomologous ways: by ossification of the median gastroid cartilage or by junction of medial extensions of the pubes and ischia (Walker, 1973).

A divided thyroid fenestra is the common condition among Recent turtles (character 104, table 18; Baur, 1891a; Zug, 1971). But the bony junction in chelydrids and *Dermatemys* occurs through ossification of the medial gastroid cartilage, a structure which is found in all open forms (Baur, 1891a). This is a minor modification of an otherwise completely open condition. Very distinct reduction and division of the thyroid fenestra occurs by extention of the pubis and ischium into the fenestra. Among living cryptodires this occurs only in *Platysternon,* kinosternine kinosternids, and testudinoids.

Baur's (1891a) interpretation of this character is that an open thyroid fenestra is primitive and a divided fenestra derived. Data from living turtles support this hypothesis. However, *Proganochelys* (Gaffney, MS), some

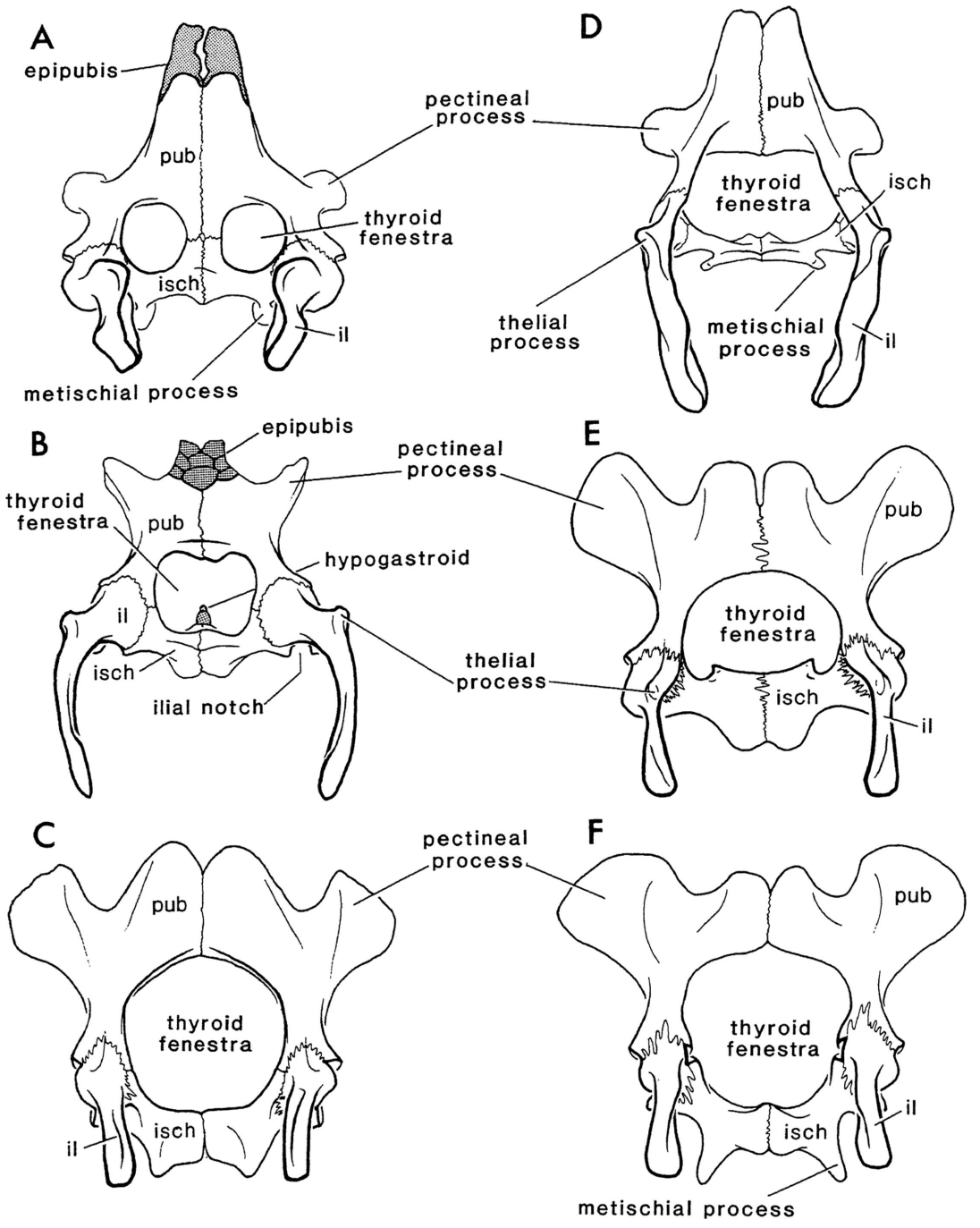

Fig. 21. Dorsal views of the pelvis of six eucryptodiran turtles. **A.** *Pseudemys nelsoni* (AMNH 129736); **B.** *Staurotypus triporcatus* (UF 13482); **C.** *Trionyx ferox* (AMNH 129737); **D.** *Carettochelys insculpta* (AMNH 84212); **E.** *Lissemys punctata* (UF 56017); **F.** *Chitra indica* (FMNH 224228). Abbreviations: **il,** ilium; **isch,** ischium; **pub,** pubis. Stippled areas represent calcified cartilage.

chelonioids, and some baenids (Hay, 1908) have the thyroid fenestra divided by ischial-pubic contact. If the divided condition is found among other extinct families, the use of global parsimony may require this state to be recognized as primitive. Should this be the case, then an open foramen could be used as a shared derived character within the Chelydridae, the Chelonioidea, and Trionychoidea. For the present, Baur's interpretation is accepted.

Baur (1891a) indicated that expansion of the undivided thyroid fenestra in trionychids is a uniquely derived condition. This fenestra is open widely, and ischial extension into it is minimal (*Dermatemys* and staurotypines, fig. 21B) or absent (most trionychids and *Carettochelys,* fig. 21D–F) in all trionychoids except for kinosternines. When the ischia do extend into the thyroid fenestra in species of the Trionychidae (fig. 21E), this is considered to occur by reversal to the primitive condition. It appears only in *Lissemys punctata, Cycloderma aubryi,* and *C. frenatum* (character 107, table 17).

Most trionychids, and in fact most cryptodires, have distinct, posteriorly directed processes of the ischia, the metischial processes (fig. 21A, D, F). In seven species of trionychids (all five living species of the Cyclanorbinae, *Trionyx euphraticus,* and *T. ferox*) these processes exist only as posteriomedial expansions of the ischia and not as free projections (fig. 21C, E). Outgroup taxa which also lack metischial processes include *Claudius, Staurotypus* (fig. 21B), some *Kinosternon,* some *Dermatemys,* and some cheloniids. Because metischial processes are present in *Carettochelys* (the proposed sister group for the Trionychidae), some members of the other two trionychoid families and most other turtles, their presence is judged to be primitive for the Trionychidae and their absence derived (character 109, tables 17, 18).

One additional character of the pelvis, which bears on the current problem only in that it supports monophyly of the Kinosternidae, is a distinct notch in the acetabulum at the junction of the ilium and ischium (fig. 21B). Such a notch is present in *Staurotypus, Claudius,* and most *Kinosternon* (character 110, table 18).

Pectoral Girdle

The pectoral girdle of all turtles is a triradiate structure composed of two elements, the scapula and coracoid. From the acetabulum the main body of the scapula extends dorsomedially to the carapace in the region of the first body vertebra. The acromion process of the scapula extends anteromedially to the plastron. The coracoid joins the scapula only at the glenoid fossa and projects posteromedially toward the midline of the plastron. The relative lengths of these three projections and the angles between them vary in a systematically useful manner. Their use in systematics up to this time appears to be limited (Meylan and Auffenberg, 1986).

In most turtles, the dorsal projection of the scapula is the longest of the three pectoral processes. The only exceptions are the chelonioids, trionychine trionychids, and *Carettochelys* in which the coracoid is longer (character 113, tables 17, 18). The shortest projection is the acromion process of the scapula except in the Testudinoidea in which the coracoid is always shortest (character 111, table 17). An exceptionally long or exceptionally short coracoid is considered to be derived.

Two angles in the pectoral girdle, one between the acromion process and main body of the scapula and the other between the acromion process and the coracoid, were measured. In most cryptodires the former angle approaches 90° and is always much greater than the latter. The same is true for majority of trionychids although the larger angle tends to be somewhat less (65–75°). In six taxa the arcomion-scapula angle is lower still and the coracoid-acromion angle is higher, so that there is little or no difference between them. The similarity of these two angles is considered to be a derived character state within the Trionychidae (character 112, table 17).

Appendicular Skeleton

The humerus and femur of trionychids are remarkably similar in general appearance. Both form gentle S-shaped curves, both have two large proximal trochanters which are free from each other, and both have weakly differentiated distal tubercles. The humerus can

be distinguished from the femur most easily by the presence of an entepicondylar groove that is always open in this family. Furthermore the lesser trochanter of the humerus lies in an anteroposterior plane that runs through the main axis of the humerus. The greater trochanter of the humerus and both trochanters of the femur lie at a high angle to this plane.

The condition of the entepicondylar foramen of the humerus is constant in the Trionychidae, but it can be open or closed in pleurodires, *Kinosternon, Dermatemys,* and among the various genera of emydids. It closes with age in chelydrids, and is apparently always closed in *Carettochelys.* It is always open in cheloniids and staurotypines. Because the closed condition is found in some members of all three outgroup trionychoid families, the consistently open condition in the Trionychidae is unique within the superfamily (character 79, table 18).

The carpus and tarsus of trionychids do not differ significantly from those of other cryptodires (Hay, 1908; Ogushi, 1911). The carpus consists of ten elements: an intermedium, ulnare, and pisiform, two centralia, and five carpals. Unlike most other turtles, the trionychids do not have the intermedium separating the distal ends of the radius and ulna; instead these forearm elements have a strong contact. The only other taxa in which this occurs are the families Cheloniidae and Testudinidae (character 81, table 18).

Among trionychids there is a uniform number of phalanges in digits one, two, and three (those which are clawed) but a variable number in digits four and five. The most common phalangeal formula for turtles is 2-3-3-3-3 (Romer, 1956). In those digits of trionychids which are clawed, 1, 2, and 3 have this number. Those which have no claws (digits 4 and 5) may differ from this most common, and according to Hay (1908), primitive number. In almost every trionychid for which an articulated manus is available the fourth digit has at least four phalanges, a few have five, and *Lissemys* and *Chitra* have as many as six. Only *Cyclanorbis senegalensis* (one specimen available) appears to retain the primitive number of three elements. Despite this exception, hyperphalangy of the fourth digit is considered to be a derived feature of the Trionychidae. Hyperphalangy of the fifth digit of the manus is less common in the Trionychidae. Although there is some interspecific variation within the data set for both of these characters, the data are not sufficient to allow use of this character in the intrafamilial analysis.

Hyperphalangy of the fourth digit of the pes is also commonplace for trionychids. There is variation among family members but, like the manus, the data are insufficient to include them in the analysis of intrafamilial relationships. Hyperphalangy is treated as a single character (character 80, table 18) and is used only in the interfamilial analyses.

DISCUSSION

HIGHER RELATIONSHIPS OF THE TRIONYCHIDAE

Monophyly of the Trionychoidea

The characters examined during the course of this study support the hypothesis that the families Dermatemydidae, Kinosternidae, Carettochelyidae, and Trionychidae form a monophyletic group. These relationships were suggested by Gaffney (1975) who assembled these families as the superfamily Trionychoidea (fig. 22). Relationship of the Trionychidae to the Kinosternidae and Dermatemydidae was first proposed late in the last century by Baur (1891a). Although it has subsequently been supported by the work of Albrecht (1967), Zug (1966, 1972), and Gaffney (1975, 1979b, 1984), it is not frequently cited (an exception is Smith and Smith, 1980). An alternative proposal for the higher relationships of turtles by Williams (1950, reproduced here as fig. 23) has received wider use (Dowling and Duellman, 1974; Goin and Goin, 1962, 1971; Porter, 1972; Pritchard,

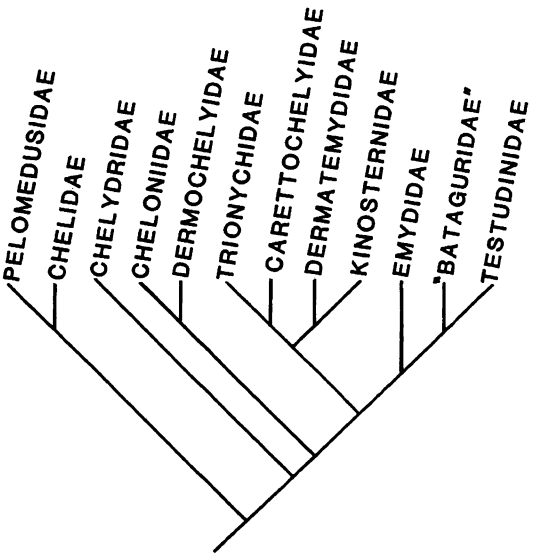

Fig. 22. A cladogram of living turtle families based on Gaffney (1984) with recognition of the Bataguridae from Hirayama (1985). Character states indicating monophyly of the Trionychoidea are enumerated in figure 24.

TABLE 19
Shared Derived Osteological Characters of the Trionychoidea

Character code	Derived state
26	at least one pair of plastral buttresses fails to reach pleurals
39	cheek emargination reduced
43	palatines contribute significantly to braincase
55	basis tuberculi basalis absent
57	canalis carotici straight and wide
61	no groove for stapedial artery on prootic or parietal
77	quadrate contribution to processus trochlearis oticum less than 50%
94	surangular always present in area articularis mandibularis
89	transverse processes of tenth body vertebra do not articulate with carapace

1979a, 1979b; Romer, 1956, 1966; Wermuth and Mertens, 1961; Zug, 1966). The Williams arrangement places the family Trionychidae alone in the superfamily Trionychoidea. The Kinosternidae (as the Kinosterninae and Staurotypinae) is included in the Chelydridae which, along with the Dermatemydidae, is considered part of the Testudinoidea (fig. 23). The Carettochelyidae is confined to its own superfamily, the Carettochelyoidea.

Gaffney (1984) summarized the evidence for using the superfamily Trionychoidea (sensu Gaffney, 1975) which until now consisted largely of characters of the cranial arteries. Additional characters of the skull, lower jaw, shell, and body vertebrae are here shown to support this inclusive view of the Trionychoidea (table 19) as the most parsimonious hypothesis for relationships among living eucryptodires. Furthermore, the criteria which Williams (1950) used to include the Kinosternidae in the Testudinoidea are shown to be plesiomorphic or subject to homoplasy.

A critical feature of Gaffney's (1975, 1984) definition of the Trionychoidea is the inclusion of the Carettochelyidae. Previously, the carettochelyids had been thought of alternatively as pleurodires (Boulenger, 1889), as the missing link between trionychids and chelonioids (Strauch, 1890), or as a link between dermatemydids and kinosternids, and the Trionychidae (Baur, 1891a; Gaffney, 1975; and others). It is abundantly clear from the present analysis that the last of these three alternatives is the one best supported by available data.

Although the present study has not reexamined characters of the cranial arteries (McDowell, 1961; Albrecht, 1967; and Gaffney, 1975, 1979b, 1984), two of the external skull characters examined do reflect the different arterial patterns that distinguish trionychoids from other cryptodires. The small size of the stapedial artery in trionychoids is reflected by the absence of any grooves or furrows to accommodate this vessel where it crosses the prootic and the descending process of the parietal (character 61). In chelydrids, emydids, and testudinids, by contrast, there is a distinct though variably developed furrow or groove for the stapedial artery. In certain taxa (*Chelydra, Melanochelys, Terrapene*) these grooves extend for long distances. In other forms, especially testudinids, they are short but deep and found only adjacent to the foramen stapediotemporale.

The second arterial feature noted here re-

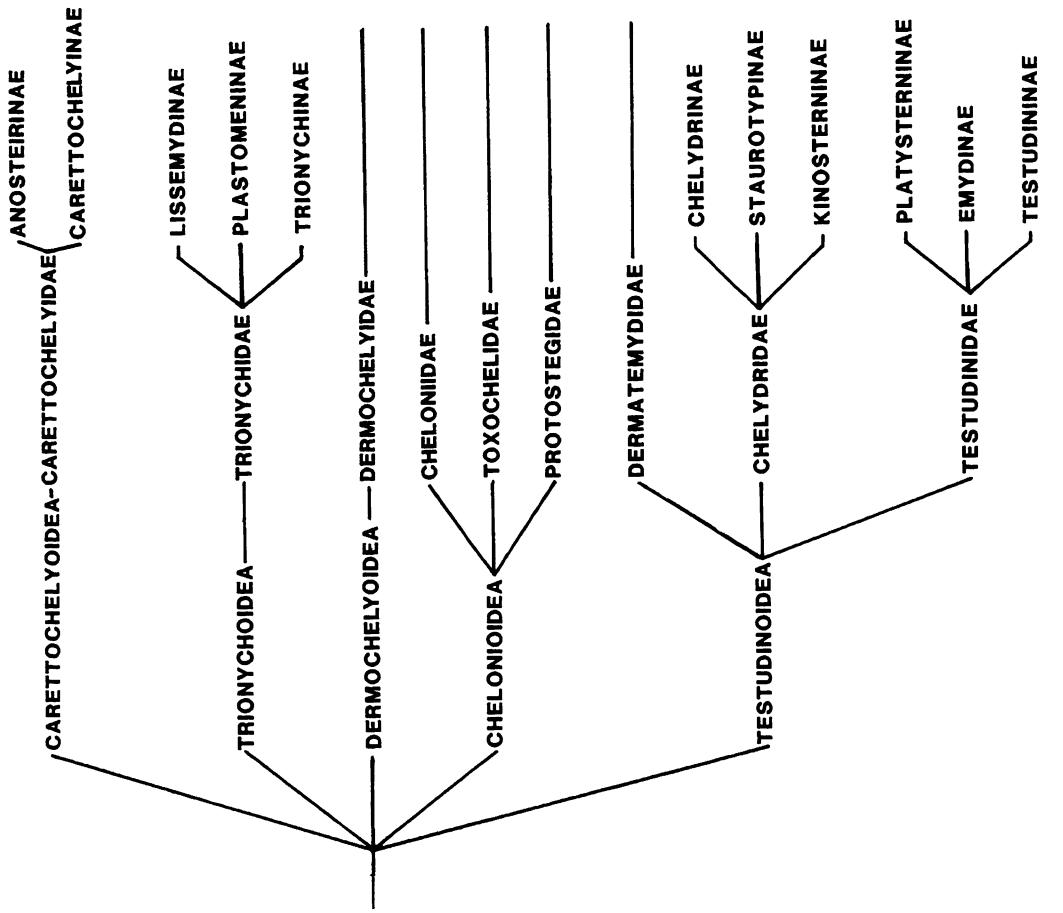

Fig. 23. A cladogram of the Testudines based on the classification in Williams (1950).

flects the increased importance of the internal carotid artery in Recent trionychoid skulls. In this superfamily, a stiff wire of a diameter just less than the foramen posterior canalis carotici interni, will pass easily from this foramen through the foramen anterior canalis carotici interni, and into the braincase (character 57). This is possible because the canalis carotici follows a very straight path. In other living cryptodires the path followed by the internal carotid artery is less direct as can be seen in figures 26–29 in Gaffney (1979b).

A useful feature of the skull used by Gaffney (1975), which does not involve blood flow pattern is the inclusion of the palatine in the lateral wall of the braincase. In essentially all turtles other than trionychoids, palatine participation is insignificant or absent (character 43) (*Morenia* and *Hardella* have a strong palatine contribution to the braincase wall, McDowell, personal commun.). In trionychoids it is quite extensive, often extending posteriorly nearly to the foramen nervi trigemini (fig. 13).

There are three additional features of the trionychoid skull which can be added to the evidence for monophyly. The cheek is solid (little cheek emargination, character 39); the dorsal surface of the basioccipital is smooth (no basis tuberculi basalis, character 55); and less than one-third of the processus trochlearis oticum is made up by the quadrate (character 77).

Among living turtles only living chelonioids (Cheloniidae, Dermochelyidae) and *Platysternon* share with the trionychoids such

limited cheek emargination. In none of these taxa does it extend above the lower rim of the orbit. Well-developed cheek emargination in the Pleurodira, baenids, pleisochelyids, and most chelydrids suggests that its absence in the Chelonioidea and Trionychoidea is derived.

The basioccipital is without a basis tubercli basalis in certain cryptodires and may be most easily explained as a single loss in the Trionychoidea and a single loss in the advanced Testudinoidea (*Rhinoclemmys* and the Testudinidae, except *Gopherus*). The small quadrate contribution to the processus trochlearis oticum also occurs in two separate monophyletic groups, the chelonioids and the trionychoids.

A single character of the lower jaw lends support to the argument for monophyly of the Trionychoidea. Throughout the superfamily there is always contribution by the surangular to the area articularis mandibularis (character 94). In certain forms it makes up the majority of this surface; in others it makes up a smaller part. It is never absent from this area, as in some testudinoids and chelydrids.

Absence of pleural contact by one or both plastral buttresses is a useful feature of the shell of trionychoids (character 26). The presence of two pairs of well-developed buttresses in the Pleurodira, Plesiochelyidae, Baenidae, and testudinoids is used here as evidence that they were present in primitive cryptodires and that absence of one or both pleural contacts can be considered derived for chelydrids, chelonioids, and trionychoids. Even if absence of plastral buttresses were the primitive condition for cryptodires, the character is still a very useful one. Testudinoids could then be recognized as having two pairs of well-developed plastral buttresses except for the most kinetic forms (*Cuora, Terrapene*). No trionychoid taxa could be included in such a group.

An important character of the posterior thoracic vertebrae is used here as evidence of monophyly of the Trionychoidea. As mentioned by Zug (1971), the tenth body vertebra, which is immediately anterior to the sacral pair, lacks contact of its transverse processes to the pleurals in members of this superfamily (fig. 6B, C). This condition occurs also in Recent chelonioids, testudinoids, and *Platysternon* (character 89). In *Chelydra* and *Macroclemys* this contact is variable. If the presence of free transverse processes of the tenth body vertebra is actually primitive, then this character would be equivalent to the alternative possibility given for the plastral buttresses above. That is, complete tenth transverse processes would be derived for the Chelonioidea and Testudinoidea and this would exclude any trionychoids from either of these superfamilies.

In summary, there are seven osteological characters, in addition to the two that correlate with cranial circulation patterns, that suggest that the Trionychoidea (sensu Gaffney, 1975) is monophyletic. The most commonly cited alternative, which places the Dermatemydidae and Kinosternidae along with the Chelydridae in the Testudinoidea, requires that all nine characters used here occur twice, once in the Trionychoidea and once in the Testudinoidea.

Observations on the morphology of the cloacal region support monophyly of the Trionychoidea. In all four families cloacal bursae are absent (Smith and James, 1958). This can be cited as additional evidence with the assumption that absence in trionychids occurs independently of absence in chelonioids and testudinids. Also, the penis in all four families of the Trionychoidea has a singly or doubly bifurcate seminal groove (Zug, 1966), a condition that occurs elsewhere only in the Testudinidae.

The evidence presented by Williams (1950) for including the Kinosternidae (as the Kinosterninae and Staurotypinae) within the Chelydridae consists of two plesiomorphic characters, and three highly variable characters. The existence of costiform processes of the nuchal is widespread among cryptodires and is most clearly visible in hatchlings and juveniles. Their retention in adults could be considered a shared derived character of the chelydrids and kinosternids but they are also retained in adult *Dermochelys, Dermatemys,* and trionychids. Their presence is probably primitive for the Cryptodira.

The evidence from the cervical formula is similarly of little value. The presence of a single biconvex vertebra and a doubly procoelous eighth cervical is used by Williams

(1950) as evidence of relationship of chelydrids and kinosternids. But these features are also present in chelonioids and dermatemydids which suggests that they are actually primitive for eucryptodires. Independent modification of this cervical formula supports monophyly of the Testudinoidea (usually two biconvex cervicals in the cervical series) and the Carettochelyidae plus Trionychidae (no biconvex cervicals, numbers two through seven opisthocoelous).

Williams (1950) cited a variable number of marginal scales, 23 or 25, as a character of his Chelydridae. The number of marginal scales reflects variation in the number of peripheral bones (Hutchison and Bramble, 1981). The Williams arrangement would require that reduction in the number of peripheral bones from 22 to 20 occur twice, once in his Testudinoidea and once in his Carettochelyoidea. In the arrangement advocated here this can be treated as a single event and as part of a transformation series which culminates in complete loss of peripherals in the Trionychidae.

Broad unridged alveolar surfaces occur in numerous unrelated taxa in addition to those included in Williams' Chelydridae. They apparently correlate with a durophagous diet (Pritchard, 1984) and do not constitute strong evidence of common ancestry of kinosternids and chelydrids. The cruciform plastron is a similarly variable character being absent within Williams' Chelydridae (many *Kinosternon* species) and present outside of this family (certain trionychine trionychids and extinct carettochelyids). There is no strong case for including the Kinosternidae within the Chelydridae on osteological grounds.

Bickham and Carr (1983) suggested that the staurotypines are the sister group of the Testudinoidea (in which they include *Platysternon*), which supports the Williams (1950) arrangement in part. These authors rely on the recognition of a homologous derived chromosome in the Staurotypinae, Emydidae, and Testudinidae. The crux of their argument is that the same microsome is fused to the same identifiable acrocentric macrosome in these three taxa. However, the combined microsome is euchromatic and homology of the short arm of their biarmed second group B macrosome seems tentative at best (see King, 1985). It is clear that their results are in irreconcilable conflict with the morphological evidence. Their observation that the Trionychoidea and Carettochelyidae have been separated from the Dermatemydidae and Kinosternidae "for a long period of time" has no bearing on the cladistic relationships of these families.

The data examined in the current study support alliance of the Kinosterninae and Staurotypinae with the other trionychoids as suggested by Baur (1891a) and advocated by Gaffney and others. Additional characters which indirectly indicate monophyly of the Trionychoidea (sensu Gaffney) are shared by members of the Kinosternidae, Carettochelyidae, and Trionychidae. But these characters suggest an alternative to the dichotomous view of the Trionychoidea used in Gaffney (1975, 1984) and shown in figure 24A.

Monophyly of the Kinosternidae, Carettochelyidae, and Trionychidae

Gaffney (1984) viewed the Trionychoidea as two clades, one the Dermatemydidae and Kinosternidae, and the other the Trionychidae and Carettochelyidae (figs. 22, 24A). Hutchison and Bramble (1981, fig. 4) detailed the relationships within the dermatemydid-kinosternid clade. They cited Albrecht (1967), Gaffney (1975), McDowell (1961), Zug (1966), and Frair (1964) for evidence of the monophyly of these two families. They did not subscribe to the idea that the Dermatemydidae and Kinosternidae share a unique common ancestor with the Trionychidae and Carettochelyidae. They believed that the evidence cited by Gaffney (1975, 1984), similarity in blood flow patterns, is convergent. As evidence they cited the presence of a large foramen stapediotemporale in *Adocus,* which they consider to be a primitive dermatemydid. A large foramen stapediotemporale appears in many trionychids but a large stapedial artery does not (Albrecht, 1967, 1976; Gaffney, 1979b). The occurrence of a large foramen stapediotemporale in these taxa is due to the retention of the primitive condition.

The osteological characters examined in the current study suggest an alternative to both the Gaffney (1975, 1984) and the Hutchison and Bramble (1981) arrangements (fig. 24B, C). Within the monophyletic Trionychoidea:

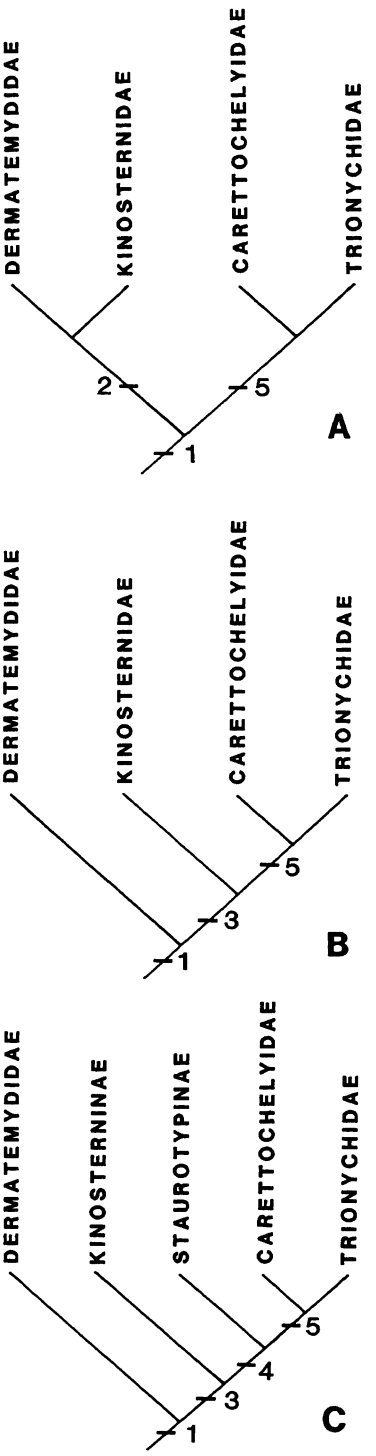

Fig. 24. Three alternative cladograms for the Trionychoidea. The distribution of character states for the numbered nodes is as follows: **Node 1:** — 26(2) one pair of plastral buttresses reaching pleurals, — 39(2) cheek emargination does not extend above ventral edge of orbit (occurs also in cheloniids, *Platysternon*, and *Malayemys*), — 43(2) palatine forms a significant part of the lateral wall of the braincase, — 55(2) basis tuberculi basalis absent (also absent in some batagurines and testudinids), — 57(2) canalis carotici interni straight and wide, — 61(2) no groove for stapedial artery present on parietal (also absent in some cheloniids), — 77(2) quadrate makes up less than one-half of processus trochlearis oticum (occurs also in chelonioids), — 89(2) transverse processes of tenth body vertebra do not reach pleurals (occurs in some chelydrids), — 94(2) surangular forms up to one-half of area articularis mandibularis. **Node 2:** — foramen stapediotemporale reduced or absent, — absence of wave-form or pedicillate sculpturing of shell surface, — enlarged palatine artery and foramen caroticum laterale. **Node 3:** — 5(2) total number of peripherals 20 or fewer, — 26(3) no plastral buttresses reach pleurals (occurs also in cheloniids and chelydrids), — 86(2) ventral process on eighth cervical double (lost in trionychids which have no ventral process on eighth cervical), — 89(3) transverse processes of body vertebrae 9 and 10 do not reach pleurals (reversed in Carettochelyidae and Trionychidae in which only tenth fails to reach pleurals), — 97(2) foramen nervi auriculotemporalis with one lateral and one dorsal opening (reversed in Carettochelyidae and Trionychidae), — 103(2) thelial process present, — 110(2) ilioischial notch present (lost in Carettochelyidae and Trionychidae). **Node 4:** — 47(2) foramen intermaxillaris present, — 107(2) ischia do not extend into thyroid fenestra of pelvic girdle. **Node 5:** Characters unique to the Carettochelyidae and Trionychidae: — 28(2) ribheads strongly sutured to vertebral centra, — 30(2) shell sculptured and lacking epidermal scutes, — 44(2) premaxillae fused, — 46(2) basisphenoid contacts palatines, — 50(3) vomer never in contact with pterygoids, — 56(2) foramen posterius canalis carotici interni completely surrounded by pterygoid, — 83(2) cervicals 2 through 7 ophisthocoelus, — 94(3) 50 percent or more of area articularis mandibularis is formed by surangular, — 99(2) retroarticular process forms about one-tenth of mandible length. Characters of the Carettochelyidae and Trionychidae which also appear in some or all living chelonioids: — 6(2) peripherals never sutured to pleurals, — 52(2) processus pterygoideus externus does not project laterally, — 81(2) radius and ulna in contact adjacent to manus, — 82(2) clawed digits of manus three or fewer, — 105(2) epipubic region never ossifies, — 113(2) coracoid longest of three pectoral processes. Characters of the Carettochelyidae and Trionychidae also found in testudinids and some chelydrids: — 37(2) incisura columella auris closed. Characters of Carettochelyidae and Trionychidae which must be reversals in cladogram presented in figure 24C: — 89(2) only the tenth body vertebra with transverse processes which do not reach the pleurals, — 97(1) foramen nervi auriculotemporalis with both openings lateral, — 110(1) ilio-ischial notch lost.

(1) the Trionychidae and Carettochelyidae share a unique common ancestor; (2) the Staurotypinae, Carettochelyidae, and Trionychidae share a common ancestor not shared by the Kinosterninae and Dermatemydidae (fig. 24C); and (3) the Dermatemydidae is the sister group to all other families of the Trionychoidea.

This arrangement is supported by 28 characters from the present study, 17 of which suggest monophyly of the Trionychidae plus Carettochelyidae (table 20). These characters can be integrated with those used by Gaffney (1984) and Hutchison and Bramble (1981) to support the arrangement shown in figure 24C as the most parsimonious for the Trionychoidea.

Monophyly of the Kinosternidae, Carettochelyidae, and Trionychidae is suggested by two characters of the shell, one of the cervical series and one of the pelvis. In all members of these three families there are 20 or fewer peripherals (character 5) and plastral buttresses lack pleural contact (character 26). The ventral process of the eighth cervical is double (fig. 19) except in the trionychids in which this process is absent (character 86). In the pelvis, a thelial process (fig. 21) is present in kinosternids and Carettochelyids but is absent in nearly all trionychids (observed only in specimens of *Lissemys,* MHNG 615.87, UMMZ 129396, UF 56017) (character 103).

The inclusion of the Trionychidae and Carettochelyidae in the same clade as the Kinosternidae in the Hutchison and Bramble (1981) arrangement requires that these taxa share the features shown to be derived for the dermatemydids plus kinosternids in that study. However, scutes are absent from all trionychids and in carettochelyids only the vertebral scutes develop and these are lost soon after hatching (Zangerl, 1959); thus the many characters of scalation used by Hutchison and Bramble (1981) do not enter into the current argument. Many of the remaining characters of their dermatemydid-kinosternid clade are shared by the Trionychidae and Carettochelyidae: posterior lobe reduced in width, stapedial artery reduced, large costiform processes, reduction of plastral bridge. Two other characters which they use, megacephaly and the tricarinate carapace, are actually quite variable within the Dermatemydidae and Kinosternidae. Megacephaly is as well developed in some trionychids (*Trionyx cartilagineus* and especially *T. subplanus*) as it is in megacephalous kinosternids (*Claudius angustatus, Sternotherus minor*). The tricarinate carapace is certainly absent in some dermatemydids and in some kinosternines. The reduction of carapacial keeling could very likely be a result of the flattening of the shell which occurs in the clade leading to trionychids.

The one remaining nonscute character which Hutchison and Bramble (1981) considered to be evidence of monophyly of the Kinosternidae plus Dermatemydidae, exclusive of the Trionychidae and Carettochelyidae, is the loss of sculpturing of the shell. There would have to be reversal in this character to allow the arrangement advocated here.

Two of the nonscute characters cited by Hutchison and Bramble (1981) for monophyly of the Kinosternidae are characters which I cite as evidence for the monophyly of the Kinosternidae, Trionychidae, and Carettochelyidae. These are the possession of 20 (or fewer) peripherals (character 5) and the presence of a double ventral process of the eighth cervical (character 86).

Other characters that these authors cite for the monophyly of the Kinosternidae do not necessarily exclude the Trionychidae and Carettochelyidae from this clade. These include: the loss of neural eight, the tendency for development of a secondary palate, and development of impressed musk ducts in the anterior peripherals.

Although most kinosternids have seven or fewer neurals, both *Staurotypus* species have eight (numbers two through nine) on occasion (UF 58976, BMNH 1871.1.7.5). Other than lacking an independent first neural or preneural this is identical to the proposed primitive number for trionychids.

The development of a secondary palate is not widespread enough among kinosternids to be a valid shared derived feature of this family. Hutchison and Bramble (1981) cited Gaffney (1979b) in support of this feature. Gaffney mentioned the presence of a secondary palate only in two genera (*Staurotypus* and *Xenochelys*). The palate in the other genera of this family are not remarkably elongate. This character is of value at a lower level

of universality (subfamily Staurotypinae) than it is assigned in the Hutchison and Bramble arrangement.

Impressed musk ducts are clearly visible on the interior surface of the anterior peripherals (usually numbers two, three, and four) of all kinosternids. In *Carettochelys,* there is no duct impression but there is a canal through the second peripheral. The interior opening of this canal is at the same level as the impressed duct in kinosternids, the exterior opening is identical in position to the anterior musk duct opening in trionychids. It is apparent that all trionychoids have anterior musk ducts which exit just dorsal to the forelimbs. In kinosternids they leave an impression in the anterior peripherals; in *Carettochelys* they leave no impression but apparently pass through the second peripheral. Trionychids have no anterior peripherals so the path of the musk duct cannot be traced in osteological material. The condition in *Carettochelys* could be viewed as a modification of that seen in the kinosternids.

From the osteological evidence it appears that the best arrangement for the Trionychoidea is to regard the Dermatemydidae as a sister group to the other three families. Furthermore, it is apparent that certain kinosternids have closer affinities to the carettochelyids and trionychids than others.

Monophyly of the Staurotypinae, Carettochelyidae, and Trionychidae

One line of evidence pursued in the present study supports monophyly of the Staurotypinae, Carettochelyidae, and Trionychidae, and evidence from Hutchison and Bramble (1981) supports this view. The palate of all three living species of staurotypines develops a foramen intermaxillaris (character 47). It does not appear until maturity but it forms in exactly the same manner as in carettochelyids and trionychids. It lies between the vomer and premaxillae with maxillae defining the lateral edges. In staurotypines it allows the symphyseal hook of the lower jaw to pass into the nasal capsule. In other cryptodires with well-developed symphyseal hooks, this region of the palate is usually deeply impressed (*Chelydra, Macroclemys, Platysternon*) or the premaxillae may be slightly divided (*Deirochelys*) but in no other turtles is there an opening comparable to the foramen intermaxillaris.

All four of the nonscute features used by Hutchison and Bramble (1981) for evidence of monophyly of the Staurotypinae are shared by the Trionychidae and Carettochelyidae. These are: (1) costal bone four spans peripheral six (carettochelyids); (2) the anterior lobe is kinetic; (3) there are very short plastral buttresses; and (4) scapular attachment is transferred from entoplastron to epiplastron. I find the second feature to be useful at a higher level and I have used it as evidence for monophyly of the Kinosternidae, Carettochelyidae, and Trionychidae. Attachment of the scapulae to the epiplastra via the acromial ligament has been verified for *Carettochelys* and the Trionychidae (Bramble and Carr, MS). This feature may occur in kinosternines only because the entoplastron is absent and thus it may not be homologous to the condition in Staurotypines, *Carettochelys,* and trionychids.

The osteological data support an arrangement of the families of the Trionychoidea that has not been considered previously. That is, monophyly of the Staurotypinae, Carettochelyidae, and Trionychidae (fig. 24C). That the entire Kinosternidae might be the sister group to the carettochelyid-trionychid clade (fig. 24B) is an alternative possibility.

Monophyly of the Kinosternidae exclusive of the Trionychidae and Carettochelyidae is suggested by four characters in addition to those treated by Hutchison and Bramble (1981). These are: (1) the presence of one dorsal and one lateral opening of the foramen nervi auriculotemporalis (character 97); (2) two, rather than one, posterior thoracic vertebrae having transverse processes that fail to reach the carapace (character 89); (3) the presence of an ilioischial notch (Zug, 1971; character 110); and (4) the presence of clasping or stridulating organs in most species. However, the most parsimonious arrangement of the osteological data results in the arrangement shown in figure 24C.

Monophyly of the Carettochelyidae and Trionychidae

Since it was first described, *Carettochelys* has often been associated with the Trionychidae (Baur, 1891b; Hummel, 1929;

TABLE 20
Shared Derived Characters of the Trionychidae and Carettochelyidae[a]

Character code	Character state
6	peripherals never sutured to pleurals
28	rib heads strongly sutured to vertebral centra
30	shell is sculptured and without epidermal scutes
44	premaxillae fused
46	basisphenoid contacts palatines
50	vomer not in contact with pterygoids
56	foramen posterius canalis carotici interni completely within pterygoid
94	50% or more of area articularis mandibularis formed by surangular
99	retroarticular process forms about one-tenth of jaw
83	cervical centra 2–7 opisthocoelous
52	processus pterygoideus not projecting
81	radius and ulna in contact adjacent to manus
82	number of clawed digits three or fewer
105	epipubic region never ossifies
113	coracoid longest of three pectoral processes
37	quadrate enclosing stapes
27	carapace not sutured to plastron

[a] States for characters 6 through 83 are unique among the Cryptodira. States for characters 52 through 113 are also found among the Chelonioidea. The state for 37 is also found in the Testudinidae and Chelydridae; that for 27 is also found in both the Chelonioidea and Chelydridae.

TABLE 21
Uniquely Derived Features of the Trionychidae

Character code	Character state
5	18 or fewer peripherals; no pygal or suprapygal
22	boomerang-shaped entoplastron
33	quadratojugal not in contact with postorbital
35	jugal contacts parietal
45	premaxillae excluded from apertura narium externum
80	hyperphylangy of manus digits 4 and 5, pes digit 4
82	three clawed digits in manus
84	centra of eighth cervical and first body vertebra not in contact
85	no ventral processes on eighth cervical
90	corpus hyoideum composed of six or eight ossifications
101	ilia curve posteriorly
106	pectineal processes in a single plane and in broad contact with plastron
108	pectineal processes equal to or wider than interpubic contact

Ramsay, 1886; Siebenrock, 1909; Walther, 1922). It is clear from the characters considered in the current study that this association is very well supported by osteological data (table 20). Ten of the features shared by these two families occur in no other cryptodire. Five others are present in these two families and among the Chelonioidea. However, the many unique features of the Chelonioidea (Gaffney, 1975, 1984) and the Trionychoidea discussed above suggest that these five character states have been attained in parallel. Three of them are states of characters which may only reflect the modification of limbs and girdles for a highly aquatic mode of life: coracoid is longest of three pectoral process (character 113); reduction in number of claws (character 82); and contact of radius and ulna adjacent to the manus (character 81). In addition to the 10 osteological characters that are unique to these two families, trionychids and carettochelyids are also the only cryptodires known to have a fleshy proboscis.

Monophyly of the Trionychidae

Monophyly of the family Trionychidae has, to my knowledge, never been questioned. All recent systematic studies treat the family as a monophyletic unit (De Broin, 1977; Gaffney, 1975, 1979b, 1984; Bickham and Carr, 1983; Meylan, 1985), but the osteological evidence for monophyly has never been compiled. Therefore, the unique features of the family are listed in table 21. In combination these synapomorphic features result in the unique overall morphology of this distinctive family of turtles.

RELATIONSHIPS AMONG THE RECENT TRIONYCHIDAE

Computer-assisted analyses of independent data sets from the skull, shell, and nonshell postcrania reveal that there are numerous possibilities for explaining the character state distributions of each data set by using hypotheses of descent that require a mini-

mum number of evolutionary steps. By recognizing unresolvable areas in the multiple, equal-length arrangements suggested by each data set, a single solution or consensus tree for that data set was obtained. These fundamental cladograms vary between data sets in the degree of resolution of interfamilial relationships, in their internal consistency (the amount of parallelism and reversal required by the distribution of the character states), and most importantly, in their topology. The relationships suggested by analysis of the skull data (fig. 26) differ from those obtained by analysis of shell data (fig. 25). The poor resolution achieved by the small nonshell postcranial data set (fig. 27) limits the comparability of the topology resulting from its analysis to that resulting from analysis of shell or skull characters.

Results of analyses of the three separate data sets (i.e., the fundamental cladograms, figs. 25–27) could not be resolved into a single general cladogram following the methods of Adams (1972) or Nelson (1979). Therefore, these results are contrasted and compared to one another and to six equally parsimonious trees (figs. 29, 30) based on an analysis of all three data sets combined. This comparison suggests a choice of two alternative trees as the best hypotheses for the relationships of soft-shelled turtles from osteological evidence (figs. 33, 34).

Evidence from Shell Morphology

A previous examination (Meylan, 1985) has indicated that there is sufficient variation in shell morphology among the shells of trionychids to allow resolution of the relationships of 20 of the 22 living species. The arrangement which resulted from that study is based on 16 characters and the most parsimonious tree was produced by hand (fig. 28). That data set has been upgraded for the current study. The present shell data matrix includes 40 percent more entries (21 characters × 22 taxa vs. 16 characters × 20 taxa). With this increase in data a search for the most parsimonious tree proved to be too time consuming by hand. A tree-producing package was used to determine the most parsimonious arrangement of the Trionychidae based on shell data. This analysis produced a dozen equally parsimonious trees. This is due entirely to alternative topologies of the unresolvable portions of the trees. Two clades that appear in all of the shortest-length trees cannot be fully resolved by analysis of the data from the shell alone. These problematical clades are a group of Cyclanorbines (*Cycloderma aubryi, Cycloderma frenatum,* and *Lissemys punctata*) and the Indian species of the genus *Trionyx.* These two clades are shown to be unresolved in the tree which best represents the relationships of the Trionychidae based on shell morphology alone (fig. 25).

These results are generally compatible with those of Meylan (1985). The monophyly of the Trionychinae is supported. Monophyly of the Indian species and its position as the sister group to the remaining Trionychinae is also repeated. The Asian species occupy the middle ground between the Indian clade and a previously recognized clade leading to the North American forms.

The most obvious divergences from the previous arrangement (Meylan, 1985) are the failure to recognize a monophyletic Cyclanorbinae and the recognition of most Asian species as a monophyletic group. In this regard these results support the conclusions of De Broin (1977) who suggested that the Cyclanorbinae may not be monophyletic and that the Trionychinae includes three monophyletic groups, the Indian forms (her *Aspiderites*), most other Asian forms (her *Amyda*), and a group which culminates in the North American forms (her *Platypeltis*).

The failure of analysis of the current shell data to support a monophyletic Cyclanorbinae, contrary to the findings in Meylan (1985), can be attributed to the inclusion of several new characters not considered in that study. *Cyclanorbis elegans* shares with the Trionychinae a reduction in length of the bony bridge and articulation of the ilia against the cartilaginous part of the shell rather than on the bony disc (characters 21 and 23). These characters work in concert with reduced plastral callosities, a short nuchal bone, and the united anterior and posterior costiform processes (characters 1, 2, and 9) to suggest that the two *Cyclanorbis* species share a unique common ancester with the Trionychinae. However, the distribution of two characters which support monophyly of the Cyclanor-

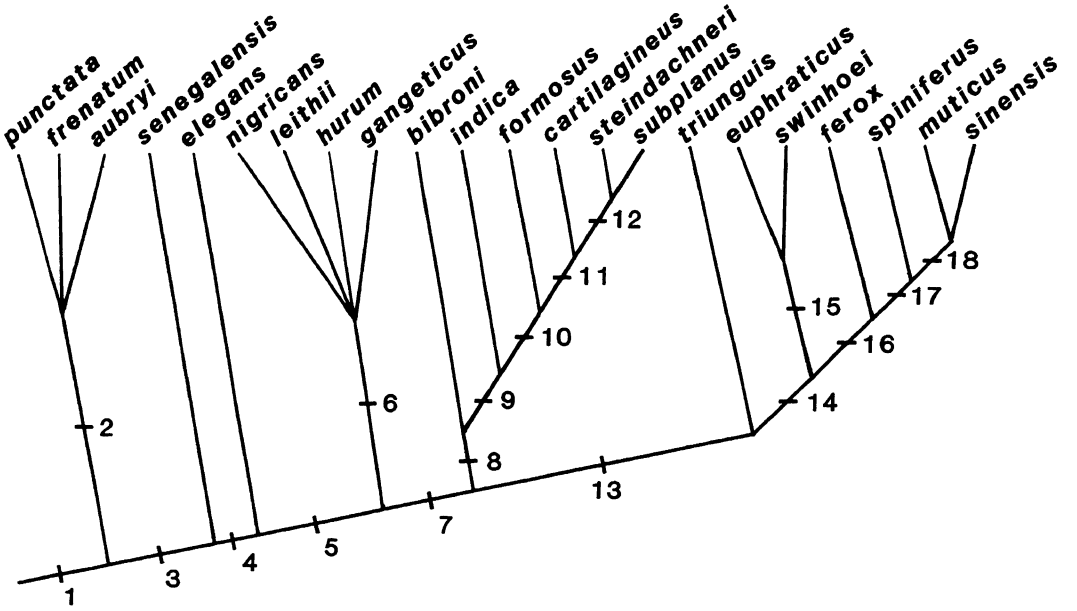

Fig. 25. The most parsimonious cladogram of extant soft-shelled turtles based on 22 characters of shell morphology. The characters defining each node are as follows: **Node 1:** — 1(2) nuchal more than two times wider than long, — 5(4) peripherals absent, — 10(2) hyo- and hypoplastra fuse just after hatching, — 13(2) posterior process of hypoplastra lateral to anterior process of xiphiplastra, — 14(2) eight or nine neurals (after reversal to primitive condition at node 9, occurs again in *steindachneri*), — 16(2) pleurals seven and eight or eight only meet on midline (after reversal at node 8, occurs again in *steindachneri*), — 17(2) point of neural reversal at neural seven, — 22(2) "boomerang-shaped" entoplastron. **Node 2:** — 19(2) epiplastra I-shaped, — 25(2) carapacial margin straight or concave posteriorly. **Node 3:** — 1(3) nuchal bone three or more times wider than long, — 2(2) anterior and posterior costiform processes united, — 3(2) anterior edge of first body vertebra located at middle of nuchal (occurs also in *aubryi*). **Node 4:** — 9(3) four or fewer plastral callosities (reverses twice), — 21(2) no depressions for the ilia on the eighth pleurals, — 23(2) bridge short. **Node 5:** — 10(1) hyo- and hypoplastra do not fuse just after hatching (a reversal), — 13(1) anterior process of xiphiplastra lateral to posterior process of hypoplastra (a reversal), — 17(3) point of neural reversal at neural six or seven or anterior. **Node 6:** — 9(2) five callosities present in plastron (a reversal that occurs also in *cartilagineus*), — 20(2) anterior projection of epiplastron of intermediate length. **Node 7:** — 4(2) first and second neurals fused. **Node 8:** — 16(1) only eighth pleurals meet on midline (a reversal). **Node 9:** — 14(1) nine neurals (fused one and two count two; a reversal). **Node 10:** — 17(2) point of neural reversal at neural seven (a reversal). **Node 11:** — 20(3) anterior process of epiplastron long. **Node 12:** — 24(2) largest adult size 200 mm or less (occurs also at node 17). **Node 13:** — 14(3) eight or fewer neurals (fused first and second count as two). **Node 14:** — 8(2) eighth pleurals reduced in size. **Node 15:** — 9(4) two plastral callosities (occurs also in *elegans*). **Node 16:** — 15(3) position of neural reversal highly variable, — 17(5) point of posteriormost neural reversal at neural four, five, or six, — 29(2) sexual dimorphism in disc size (occurs also in *indica*). **Node 17:** — 9(1) up to seven callosities present in plastron (a reversal). **Node 18:** — 1(4) nuchal four or more times wider than long (occurs also in *subplanus*), — 14(2) eight or nine neurals present (a reversal; fused one and two count two). Species characters: *punctata:* — 5(3) 14 to 18 peripherals present, — 7(2) prenuchal bone present (occurs also in *senegalensis*), — 14(4) seven or eight neurals present. *aubryi:* — 3(2) anterior edge of first body vertebra at middle of nuchal (occurs also at node 3), — 17(1) neural reversal occurs at neural eight (a reversal which occurs also in *elegans*). *senegalensis:* — 7(2) prenuchal bone present (occurs also in *punctata*), — 9(0) nine or more callosities in the plastron, — 14(5) seven or fewer neurals, — 16(4) additional pleurals to six, seven and eight meet at midline. *elegans:* — 1(2) nuchal two times wider than long (a reversal that also occurs in *formosus*

Fig. 25 (*continued*).
and *steindachneri*), — 9(4) two plastral callosities (occurs also at node 15), — 17(1) neural reversal occurs at neural eight (a reversal that occurs also in *aubryi*). *indica:* — 3(3) anterior edge of first body vertebra occurs at anterior edge of nuchal, — 29(2) sexual dimorphism in disc length (occurs also at node 16). *formosus:* — 1(2) nuchal two times wider than long (a reversal that occurs also in *elegans* and *steindachneri*). *cartilagineus:* — 9(2) five callosities in plastron (a reversal that occurs also at node 6). *steindachneri:* — 1(2) nuchal two times wider than long (a reversal that occurs also in *elegans* and *formosus*), — 14(2) eight or nine neurals (fused one and two count two), — 16(2) pleurals seven and eight or eight only meet at midline (a rederived feature after reversal to the primitive condition at node 8). *subplanus:* — 1(4) nuchal four times wider than long (occurs also at node 18), — 15(2) point of neural reversal is always at adjacent neurals (also in *hurum* and *gangeticus*), — 16(0) no pleurals meet on midline. *sinensis:* — 8(1) eighth pleurals not reduced in size (a reversal), — 20(3) anterior process of epiplastra long, — 29(1) no sexual dimorphism (a reversal).

binae (characters 10 and 13) in Meylan, 1985, are explained as unique reversals to the primitive condition for all trionychines in figure 25. Characters of the skull and nonshell postcrania considered below and the results from all three data sets analyzed together firmly support monophyly of the Cyclanorbinae and the recognition of this subfamily.

In the arrangement based on shell morphology, monophyly of the Indian species is supported by the occurrence of five plastral callosities in all species (character 9) (this occurs elsewhere only in *Trionyx cartilagineus*) and on the occurrence of epiplastral projections of intermediate length (character 20). It is also possible that the existence of two neurals between the first pleurals is a derived feature arrived at independently in the Cyclanorbinae and the Indian forms.

Monophyly of the Asian clade (*Pelochelys bibroni* through *Trionyx subplanus*) in figure 25 is supported only by an apparent reversal. The eighth pleurals are the only pair that meet on the midline, a condition which occurs elsewhere only in *Trionyx leithii*. Monophyly of *T. triunguis, T. euphraticus, T. swinhoei,* the three North American forms, and *T. sinensis,* is suggested by a unique reduction in the total number of neurals (character 14) although there is a reversal in this condition in the most derived forms.

Evidence from Skull Morphology

Like variation in the trionychid shell, variation in the trionychid skull is sufficient to allow nearly complete resolution of the relationships of all 22 living species.

Analysis of 23 characters of the trionychid skull using PAUP results in a minimum-length tree of 99 evolutionary steps. Three equally parsimonious trees produced by PAUP differ only in minor changes in the positions of *Trionyx formosus* and *T. leithii.* Variation in the three trees is represented in the single solution cladogram by a trichotomy (fig. 26). The three equally parsimonious cladograms otherwise agree completely in the remainder of their structure.

The three arrangements all support a monophyletic Cyclanorbinae as the sister group to a monophyletic Trionychinae. *Lissemys punctata* is always the sister group to all other cyclanorbines. *Chitra indica* and *Pelochelys bibroni* form a clade which is the sister group to the remaining Trionychinae. *Trionyx cartilagineus* is the sister group to two remaining major monophyletic units, the North American group plus *T. triunguis, T. euphraticus,* and *T. swinhoei* on the one hand, and the Indian and Asian *Trionyx* species on the other. Unlike the arrangement based on shell morphology, *T. sinensis* is placed among the Asian clade and *T. subplanus* is the sister group to the North American clade.

Although the arrangement based on skull data alone is initially more appealing for several reasons, its internal consistency is lower than that derived from shell data. The distribution of nearly two-thirds of the character states in the skull cladogram must be explained by reversal or parallelism. The appealing features of the skull arrangement include its support of both subfamilies, the Cyclanorbinae and Trionychinae, as monophyletic units and its overall similarity to the arrangement in Meylan (1985) which in turn approaches arrangements proposed by Loveridge and Williams (1957) and De Broin (1977).

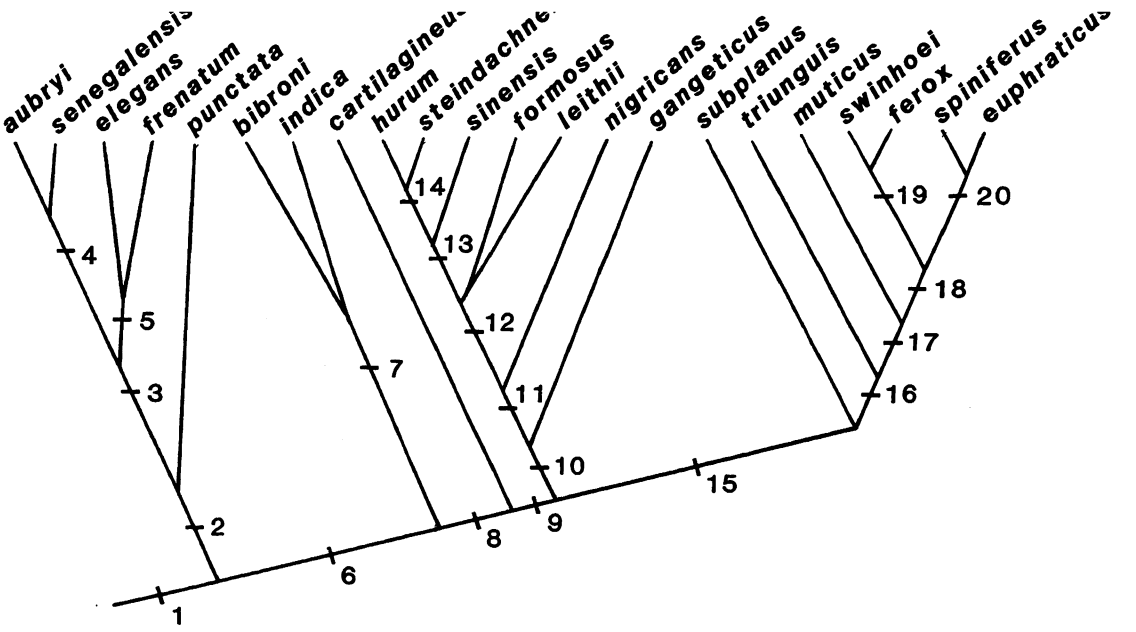

Fig. 26. The distribution of character states in the most parsimonious arrangement of extant soft-shelled turtles based on 23 characters of skull morphology. Evidence for the numbered nodes is as follows: **Node 1:** — 33(2) quadratojugal never contacts postorbital, — 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs independently in *subplanus* and *muticus* after reversal at node 8), — 35(2) jugal always contacts parietal within temporal fossa, — 45(2) premaxillae always excluded from apertura narium externum, — 48(2) vomer never divides maxillae, — 53(2) foramen palatinum posterius small, — 60(2) foramen posterius canalis carotici interni within lateral crest of basioccipital tubercle, — 68(2) epipterygoid, when present, contacts palatine in one-half of sample. **Node 2:** — 54(2) foramen palatinum posterius forms in palatine only (occurs also in *sinensis* and *swinhoei*), — 58(2) foramen jugulare posterius excluded from fenestra postotica by pterygoid arching dorsally to contact opisthotic, — 60(3) foramen posterius canalis carotici interni below lateral crest of basioccipital tubercle (occurs also at node 9). **Node 3:** — 34(3) jugal always contacts parietal on skull surface (also occurs at node 7 and in *formosus*), — 36(2) vomer does not contact prefrontal (occurs also in *indica*, reverses in *elegans*), — 49(2) vomer never reaches intermaxillary foramen (occurs also at node 8), — 53(3) foramen palatinum posterius small and divided, — 69(2) no contact between pterygoid and foramen nervi trigemini when epipterygoid is present (occurs also in *muticus*), — 72(2) epipterygoid contacts prootic posterior to foramen nervi trigemini. **Node 4:** — 41(2) dorsal edge of apertura narium externum weakly emarginate laterally (occurs also at node 8). **Node 5:** — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also at node 6), — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at node 8). **Node 6:** — 70(0) when epipterygoid is present pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all, — 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in one-half of sample (reverses at node 9), — 73(2) epipterygoid fuses to pterygoid only in adults (occurs also at node 5). **Node 7:** — 34(3) jugal always contacts parietal on skull surface (occurs also at node 3 and in *formosus*), — 48(1) vomer divides maxillae (a reversal), — 68(3) epipterygoid never contacts palatine (occurs also in *senegalensis* and *frenatum*). **Node 8:** — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at node 5 and in *formosus*), — 34(1) jugal never contacts parietal on skull surface (a unique reversal), — 41(2) dorsal edge of apertura narium externum weakly laterally emarginate (occurs also at node 4), — 49(2) vomer never reaches intermaxillary foramen (occurs also at node 3), — 64(2) basisphenoid sometimes medially constricted (occurs also at node 20 after reversal at node 16). **Node 9:** — 60(3) foramen posterius canalis carotici interni below lateral crest of basioccipital tubercle (occurs also at node 2), — 68(1) epipterygoid, when present, always in contact with palatine (a reversal that occurs also in *elegans*), — 71(1) epipterygoid never contacts prootic anterior to foramen nervi trigemini (a unique reversal). **Node 10:** — 64(3) basisphenoid always medially constricted, — 70(1) when epipterygoid is present pterygoid contacts foramen nervi trigemini between prootic and epipterygoid or not at all (a presumed reversal). **Node 11:** — 76(1) quadratojugal never participates in proces-

Fig. 26 (*continued*).

sus trochlearis oticum (a unique reversal), — 32(2) jugal contacts squamosal in one-half of sample (occurs also in *muticus* and *swinhoei*), — 73(3) epipterygoid never fuses to pterygoid (occurs also at node 18, in *cartilagineus* and in *indica*). **Node 12:** — 34(2) jugal contacts parietal on skull roof in one-half of sample (occurs also at node 1, in *subplanus* and in *muticus*). **Node 13:** — 41(3) dorsal edge of apertura narium externum strongly laterally emarginate (occurs also at node 15), — 59(2) foramen jugularis posterius excluded from fenestra postotica by descending process of opisthotic which reaches pterygoid (occurs also in *subplanus*, absent in *hurum*). **Node 14:** — 31(1) quadratojugal contacts maxillary (a unique reversal), — 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in 50% of sample (occurs also in *cartilagineus, bibroni,* and *indica*). **Node 15:** — 41(3) dorsal edge of apertura narium externum strongly laterally emarginate (occurs also at node 13). **Node 16:** — 78(2) parietal makes up 22.1% or more of the processus trochlearis oticum (occurs also in *nigricans* and *elegans*), — 64(1) basisphenoid not medially constricted in ventral view (a unique reversal). **Node 17:** — 48(2) vomer usually divides maxillae (a unique reversal), — 74(2) intermaxillary foramen extends across 60 percent of primary palate. **Node 18:** — 49(1) vomer reaches intermaxillary foramen (a reversal that occurs also in *senegalensis*), — 73(3) epipterygoid never fuses to pterygoid (occurs also at node 11 and in *cartilagineus* and *indica*). **Node 19:** — 48(1) vomer always divides maxillae (a reversal that also occurs at node 7 and in *senegalensis*). **Node 20:** — 64(2) basisphenoid constricted in some individuals (occurs also in *cartilagineus* and *subplanus*). Species characters. *aubryi:* — 53(4) foramen palatinum posterius divided into many small openings (occurs also in *frenatum*), — 65(2) premaxilla absent in some individuals. *senegalensis:* — 48(1) vomer always divides maxillae (occurs also at nodes 7 and 19), — 49(1) vomer reaches intermaxillary foramen (occurs also at node 18), — 68(3) epipterygoid, when present, never contacts palatine (occurs also at node 7, in *frenatum* and *nigricans*). *elegans:* — 36(1) vomer contacts prefrontals (a unique reversal), — 68(1) epipterygoid, if present, always contacts the palatine (occurs also at node 9). *frenatum:* — 53(4) foramen palatinum posterius consists of many small openings (occurs also in *aubryi*), — 68(3) epipterygoid, if present, never contacts the palatine (occurs also at node 7, in *nigricans* and *senegalensis*). *indica:* — 36(2) vomer never contacts prefrontal (occurs also at node 3), — 65(3) premaxilla usually absent, — 71(3) epipterygoid always contacts prootic anterior to foramen nervi trigemini (occurs also in *steindachneri*), — 73(3) epipterygoid never fuses to pterygoid (occurs also at nodes 11 and 18 and in *cartilagineus*), — 74(0) intermaxillary foramen less than 7 percent of primary palate length, — 75(0) postorbital bar twice length of orbit. *cartilagineus:* — 73(3) epipterygoid never fuses to pterygoid (occurs also at nodes 11 and 18 and in *indica*). *hurum:* — 59(1) foramen jugulare posterius not excluded from fenestra postotica (a reversal). *steindachneri:* — 34(3) jugal always contacts parietal on skull surface (occurs also at nodes 3 and 7 and in *formosus*), — 71(3) epipterygoid always contacts prootic anterior to foramen nervi trigemini (occurs also in *indica*), — 75(2) postorbital bar very narrow, less than one-fifth orbit width (occurs also in *muticus, spiniferus,* and *subplanus*). *sinensis:* — 54(2) foramen palatinum posterius forms in palatine only (occurs at node 2 and in *swinhoei*), — 70(2) when epipterygoid is present pterygoid contacts foramen nervi trigemini between epipterygoid and parietal or not at all — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at nodes 5 and 9). *formosus:* — 34(3) jugal always contacts parietal on skull surface (occurs at nodes 3 and 7 and in *steindachneri*). *leithii:* — 70(0) when epipterygoid is present, pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all (occurs also at node 6). *nigricans:* — 60(2) foramen posterius canalis carotici interni located in lateral crest of basioccipital tubercle (occurs also in *bibroni, cartilagineus,* and *indica*), — 68(3) epipterygoid, when present, never contacts palatine (occurs also at node 7 and in *senegalensis*), — 78(2) parietal makes up 22.1% or more of processus trochlearis oticum (occurs also at node 16 and in *elegans*). *subplanus:* — 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 12, in *punctata* and in *muticus*), — 59(2) foramen juglare posterius excluded from fenestra postotica by descending process of opisthotic (occurs also at node 13), — 75(2) postorbital bar less than one-fifth of orbit width (occurs also in *spiniferus, muticus,* and *sinensis*). *muticus:* — 32(2) jugal contacts squamosal in one-half of sample (occurs also at node 11 and in *swinhoei*), — 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 12, in *punctata* and *subplanus*), — 69(2) contact between pterygoid and foramen nervi trigemini never occurs when epipterygoid is present (occurs also at node 3 and in *steindachneri*), — 75(2) postorbital bar less than one-fifth of orbit width (occurs also in *spiniferus, sinensis,* and *subplanus*. *swinhoei:* — 32(2) jugal contacts squamosal in one-half of sample (occurs also at node 11 and in *muticus*), — 41(2) dorsal edge of apertura narium externum weakly laterally emarginate (a reversal that occurs elsewhere only in *euphratricus*), — 54(2) foramen palatinum posterius forms in palatine only (occurs also at node 2 and in *sinensis*). *spiniferus:* — 75(2) postorbital bar less than one-fifth of orbit width (occurs also in *sinensis, muticus,* and *subplanus*), — 70(2) when epipterygoid is present, pterygoid contacts foramen nervi trigemini between epipterygoid and parietal or not at all (occurs also in *sinensis*). *euphraticus:* — 41(2) dorsal edge of apertura nariun externum weakly laterally emarginate, a reversal that occurs elsewhere only in *swinhoei*).

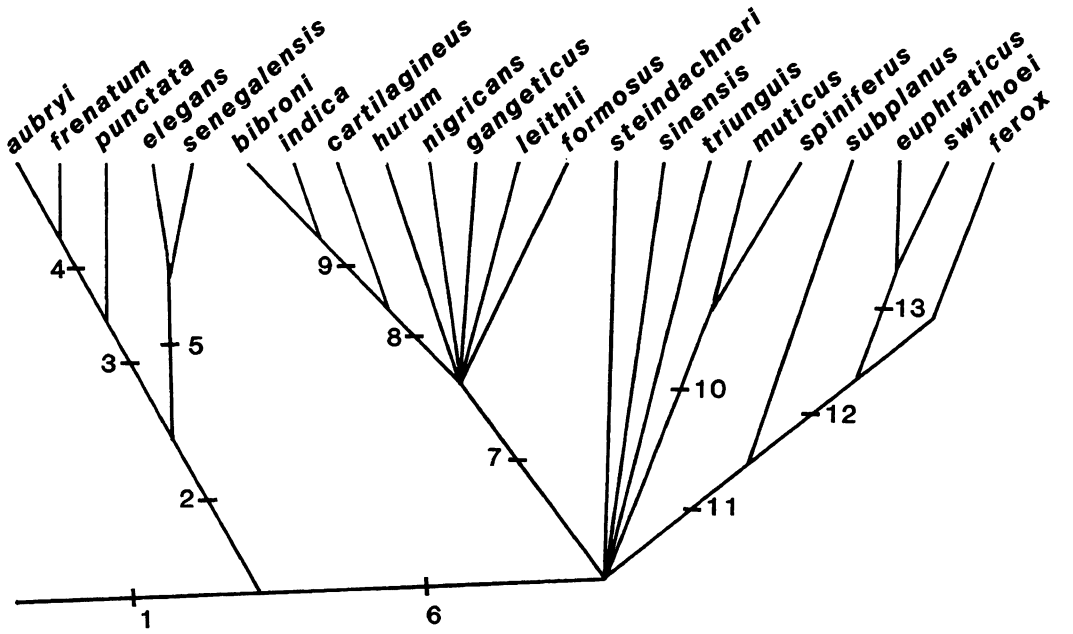

Fig. 27. The most parsimonious cladogram for extant soft-shelled turtles based on 13 characters of the mandible and nonshell postcrania. Evidence for each node is as follows: **Node 1:** — 79(3) entepicondylar foramen never closed (occurs also in the Staurotypinae and in Cheloniidae), — 80(2) hyperphalangy of manus digits 4 and 5, pes digit 4 (absent only in *senegalensis*), — 82(2) three digits clawed, — 84(2) centrum of eighth cervical not in contact with centrum of first body vertebra, — 85(2) no ventral process of eighth cervical, — 90(2) six or more ossifications in corpus hyoideum, — 96(2) foramen nervi auriculotemporalis usually with two lateral openings (occurs also in emydids and some pleurodires), — 101(2) ilia curve posteriorly, — 102(2) ilia are not expanded distally (occurs also in all Kinosternidae), — 106(2) pectineal processes and interpubic suture lie in a single plane (occurs also in *Claudius*), — 108(2) pectineal processes equal to or wider than interpubic contact. **Node 2:** — 93(2) basihyals in close contact and projecting anteriorly, — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also in *indica, formosus,* and *swinhoei*), — 109(2) metischial processes very weakly developed (occurs also at node 12). **Node 3:** — 107(1) ischia extend slightly into thyroid fenestra (reversal of feature shared by Staurotypinae, Carettochelyidae, and Trionychidae). **Node 4:** — 88(2) strong dorsal processes present on posterior cervicals. **Node 5:** — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 9 and 10). **Node 6:** — 91(2) two or more ossifications in second branchial horn, — 113(2) coracoid longest of three pectoral processes (occurs also in *punctata*). **Node 7:** — 95(2) a strong ridge present in a depression on the symphysis. **Node 8:** — 87(2) a distinct ventral keel present on the posterior end of the eighth cervical (occurs also at node 13), — 90(3) eight ossifications in corpus hyoidis (occurs also at node 11 and in *gangeticus*). **Node 9:** — 88(2) strong dorsal processes on posterior cervicals (occurs also at node 4), — 92(2) ossifications of second branchial horn very broad and strongly sutured, — 95(1) no ridge on symphysis (a unique reversal), — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 5 and 10). **Node 10:** — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 5 and 9). **Node 11:** — 90(3) eight ossifications in corpus hyoidis (occurs also at node 8 and in *gangeticus*). **Node 12:** — 91(3) seven or more ossifications in second branchial horn (occurs also in *gangeticus* and *spiniferus*), — 109(2) metischial processes not well developed (occurs also at node 2). **Node 13:** — 87(2) distinct ventral keel on posterior end of eighth cervical (occurs also at node 8). Specific characters. *punctatus:* — 113(2) coracoid longest of three pectoral processes (occurs also at node 6). *indica:* — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2 and in *formosus* and *swinhoei*). *hurum:* — 91(1) only one ossification in second branchial horn (a unique reversal). *gangeticus:* — 90(3) eight ossifications

Fig. 27 (*continued*).
in corpus hyoidis (occurs also at node 8 and node 11), — 91(3) seven or more ossifications in the second branchial horn (occurs also at node 12 and in *spiniferus*). *formosus:* — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2 and in *indica* and *swinhoei*). *spiniferus:* — 91(3) seven or more ossifications in second branchial horn (occurs also at node 12 and in *gangeticus*). *swinhoei:* — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2 and in *indica* and *formosus*).

Evidence from Nonshell Postcrania and Lower Jaw

Only 13 characters of the lower jaw and nonshell postcrania were found to display useful interspecific variation among living trionychids. This is far too few to allow complete resolution of the relationships of the Recent Trionychidae. Two pairs of species share identical character state distributions (*Cycloderma aubryi* and *Cycloderma frenatum*; *Trionyx nigricans* and *T. leithii*) and three other species share another distribution (*T. steindachneri, T. sinensis,* and *T. triunguis*). Furthermore, two additional species, *T. swinhoei* and *T. formosus,* have numerous missing values. The lack of resolvability and the presence of many missing values result in hundreds of equally parsimonious trees. But even among the numerous trees are some consistently repeated nodes.

Examination of a large subset (N = 45) of these trees reveals that nine clades appear in every one. These provide important evidence for intrafamilial relationships and are shown in a consensus tree (fig. 27). Most importantly, the Cyclanorbinae and Trionychinae are recognized in every case. The former has a unique configuration of the corpus hyoidis (character 93), lacks distinct metischial processes (character 109), and never has the foramen intermandibularis caudalis defined by bone (character 98). The latter has multiple ossifications of the second branchial horn (character 91) and the coracoid is longer than the scapula (character 113) in every case (and also in *Lissemys punctata*).

A unique reversal to the primitive condition of ischial projections into the thyroid fenestra (character 107) and reduction of the acromion process to scapula angle (character 112), each identify a separate clade within the Cyclanorbinae.

Among the Trionychinae, one large subset of taxa, the four Indian species plus *Trionyx formosus, T. cartilagineus, Chitra indica,* and *Pelochelys bibroni* are recognized as a single clade largely on the basis of a symphyseal ridge (character 95). Four characters of the nonshell postcrania support monophyly of *Chitra* and *Pelochelys.*

The remaining trionychine species always include three additional clades. *Trionyx muticus* and *T. spiniferus* share a rare configuration of the scapula (character 112). *T. subplanus, T. euphraticus, T. swinhoei,* and *T. ferox* have eight ossifications of the corpus hyoidis (character 90), also found in *T. cartilagineus, Chitra,* and *Pelochelys. T. euphraticus* and *T. ferox* have a high number of ossifications in the second branchial horn (character 91) and lack distinct methishial processes (character 109).

Although variation in the characters of the lower jaw and nonshell postcrania are insufficient to allow formulation of an independent arrangement of the Recent trionychids, certain of these characters are important in corroborating clades identified by the shell and skull data sets. Also, some characters which have proven unimportant at this level are essential to formulation of a hypothesis for the higher relationships of the Trionychidae.

Formulation of a General Hypothesis of Relationships for the Trionychidae

The methods available for constructing consensus trees (Adams, 1972 and Nelson, 1979) will not completely resolve the relationships among Recent soft-shelled turtles. The Adams (1972) method combines information from nodes present in every rival tree. There is only one node, that representing the Trionychinae, found in all three fundamental cladograms. The Nelson (1979) method combines replicated nodes as the foundation for a consensus tree; uncombinable nodes are discarded and combinable nodes, which are unreplicated but compatible with one another, are added to the replicated nodes. Only six

nodes are replicated in two or more of the fundamental cladograms in this study and four combinations of combinable unreplicated nodes can be added to produce a consensus tree which contains an equal amount of cladistic information (an equal number of nodes).

As an alternative, I have made a clade-by-clade comparison of the trees resulting from analysis of the shell data (fig. 25) to that resulting from the data on the skull (fig. 26) and the mandible and nonshell postcrania (fig. 27). These results are then compared to those based on a separate PAUP analysis of all three data sets combined (figs. 33, 34).

All three cladograms based on independent data sets and those from the combined data set consist of basal cyclanorbines, and a series of similar combinations of Indian, Asian, and North American species. It is simplest to compare and combine results by proceeding up the cladogram.

CYCLANORBINAE: Monophyly of the Cyclanorbinae has been advocated by several students of trionychid systematics (Boulenger, 1889; Deraniyagala, 1939; Loveridge and Williams, 1957; Meylan, 1985). It is supported strongly by the skull and nonshell data sets (figs. 26, 27) but does not appear in the arrangement based on the shell alone (fig. 25). As pointed out in Meylan (1985) the unique cyclanorbine xiphiplastral-hypoplastral joint and early fusion of the hyo- and hypoplastra (characters 10, 13) can be considered shared derived characters for the subfamily rather than unique reversals for the Trionychinae as shown in figure 25. These two characters, in combination with the unique cyclanorbine hyoid (character 93) restriction of the fenestra postotica by an ascending pterygoid arch (character 58), the absence of distinct metishial processes (character 109), and other characters of the skeleton and soft parts (including femoral flaps) suggest that recognition of a monophyletic Cyclanorbinae would ultimately lead to a more parsimonious arrangement of the Trionychidae. If the shell arrangement (fig. 25) is used, the distribution of seven nonshell characters common to these five taxa would require 21 evolutionary steps. On the other hand addition of the shell data to the skull arrangement would require only seven added steps, provided that the genus *Cyclanorbis* (*elegans* plus *senegalensis*) is considered to be monophyletic. Monophyly of the Cyclanorbinae is indicated in all six equally parsimonious trees based on the combined data set.

Resolution of the Cyclanorbinae is best completed by recognizing three monophyletic genera, *Lissemys* (*L. punctata*), *Cyclanorbis,* and *Cycloderma* (*aubryi* plus *frenatum*), with *Lissemys* being the sister group to the other genera. This arrangement requires that two steps be added to account for independent acquisition of epiplastron shape and shell shape (characters 19 and 25) in *Lissemys* and *Cycloderma.* But the retention of the shell topology would require independent acquisition of seven characters in *Cycloderma* and *Cyclanorbis* and would add seven evolutionary steps. Among the characters supporting monophyly of *Cyclanorbis* plus *Cycloderma* are the reduced size of the coracoid (character 113), medial curvature of the ilia (lost in *Cyclanorbis elegans*; character 109), the presence of a small and multiply divided foramen palatinum posterius (character 53), and exclusion of the quadrate from the trigeminal foramen by the epipterygoid (character 71). Three of the four species also lack prefrontal-vomer contact, an absence found elsewhere only in *Chitra indica* (character 36).

Monophyly of *Cyclanorbis* is suggested by ischial extension into the thyroid fenestra (character 107), reduced angle of the acromion process to body of scapula (character 112), wide nuchal (character 1), united costiform processes (character 2), and the location of the first thoracic vertebra in the middle of the nuchal bone (character 3). *Cycloderma* has a unique condition of the foramen palatinum posterius: it is represented by many very fine openings hardly distinguishable from the nutritive foramina of the palate (character 53). The two species of the genus also share characters of shell shape and epiplastron shape (characters 19, 25), which are found also in *Lissemys,* and the presence of enlarged dorsal processes on the cervical series which occur elsewhere only in *Chitra indica* and *Pelochelys bibroni* (character 88).

The six equally parsimonious cladograms for the combined data set match three arrangements of the Cyclanorbinae (fig. 29) to two arrangements of the Trionychinae (fig.

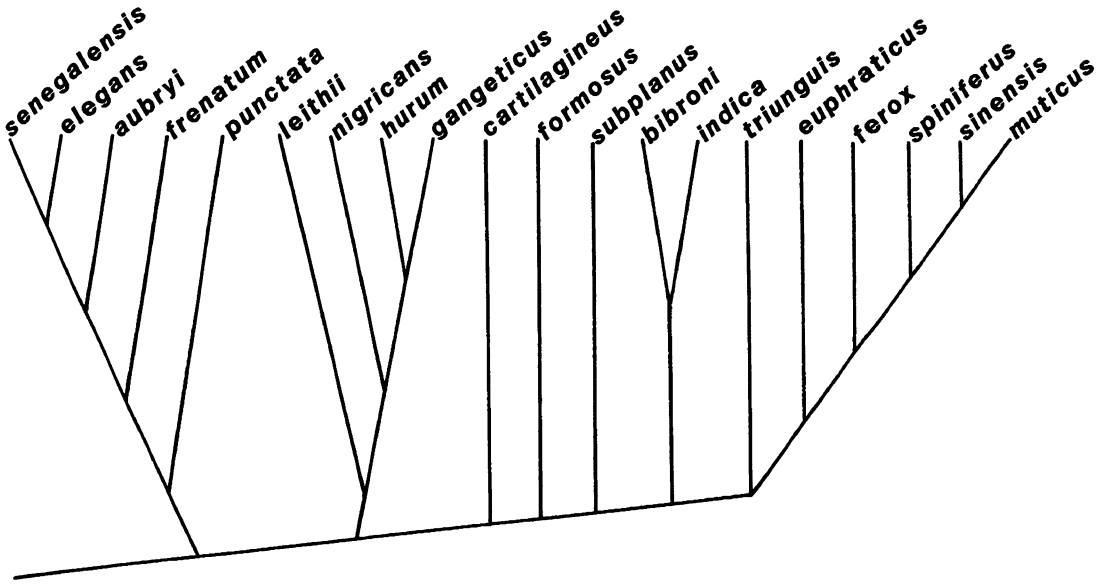

Fig. 28. A cladogram of 20 living species of soft-shelled turtles from Meylan (1985). It is based on 16 characters of the shell, a subset of those shell characters used in the current study. Evidence for the nodes is given in Meylan (1985).

30). One of the alternative cyclanorbine arrangements is that advocated above (fig. 29B). The other two require either a paraphyletic *Cyclanorbis* or a paraphyletic *Cycloderma.*

Choice between these equally parsimonious arrangements for the Cyclanorbinae rests on further considerations of the characters. Variability in the number of pleurals that meet on the midline (character 16) provides useful data that enhance the argument for recognition of a monophyletic *Cyclanorbis.* The modal condition of the neural series was used to score taxa in table 3. However, the highly derived condition (state 4 of character 16), common in *Cyclanorbis senegalensis,* is also known to occur in *Cyclanorbis elegans* (see section on neurals under variation in shell morphology). Using Cartmill's (1978) philosophy, that occasionally derived is in fact derived, the rare occurrence of a high number of pleurals meeting at the midline in *Cyclanorbis elegans* reinforces the suggestion of monophyly for this genus which appears in two of the three alternative topologies for the Cyclanorbinae (fig. 29).

Recognition of a monophyletic *Cyclanorbis* reduces the choice of topologies for the Cyclanorbinae to those shown in figure 29B and C. Examination of the characters which support monophyly of *Cycloderma* (fig. 29B) versus those which support monophyly of *Cycloderma aubryi* plus *Cyclanorbis* (fig. 29C) provides useful results relevant to determining the relative reliability of these two alternative arrangements. The two characters which argue for monophyly of *Cycloderma* include one unique evolutionary event, the reduction of the foramen palatinum posterius to a series of fine openings (character 53), and a feature which occurs elsewhere on only one occasion, the presence of large dorsal spines on the cervical vertebrae (fig. 20, character 88). The average consistency of these characters is 0.750. The average consistency of the three characters which support monophyly of *Cycloderma aubryi* and *Cyclanorbis* (fig. 29C) is much less, 0.431. These include anterior location of the first thoracic vertebra (character 3, C = 0.667), location of neural reversal (character 17, C = 0.375), and emargination of the prefrontals in the apertura narium externum (character 41, C = 0.250). On the strength of its higher consistency at the critical level (see Wheeler, 1986), it is suggested that the arrangement of the Cyclanorbinae that appears in figure 29B is the most reliable hypothesis.

TRIONYCHINAE: The shell (fig. 25) and both

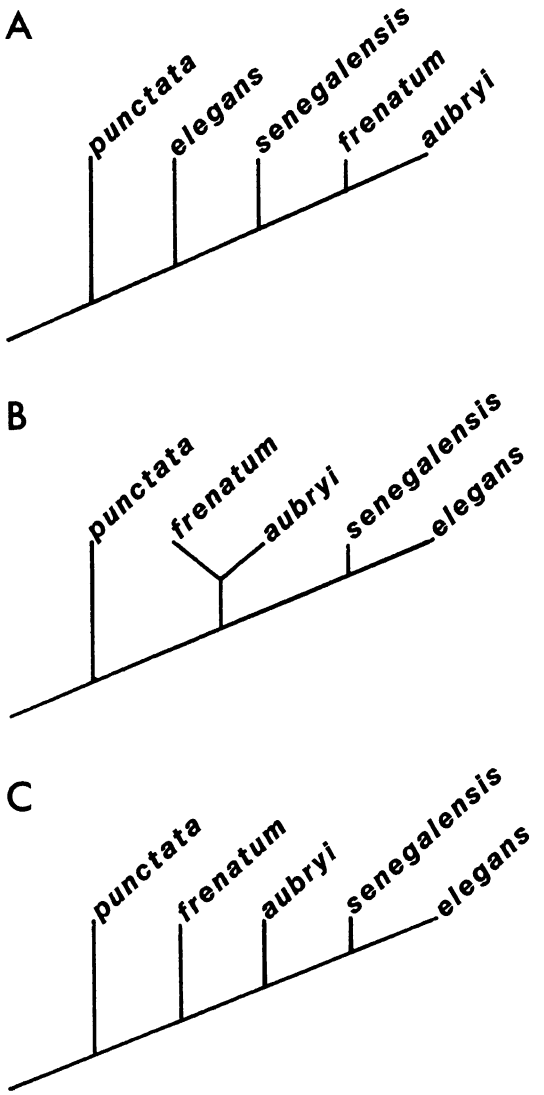

Fig. 29. The three alternative topologies for the subfamily Cyclanorbinae, each of which appears in two of six equally parsimonious cladograms of the Trionychidae based on combined skull, shell, and nonshell postcranial evidence. Based on details of character 16 and higher internal consistency of critical characters, alternative B is used in the solution cladogram.

nonshell arrangements (figs. 26, 27) support a monophyletic Trionychinae. In all, nine characters support the recognition of this subfamily (figs. 33, 34). Unique features of the Trionychinae include advancement of the point of reversal of neural orientation at least to neural six or seven and the presence of multiple ossifications of the second branchial horn (characters 17 and 91). Four other features of the Trionychinae appear independently in one or both *Cyclanorbis* species (characters 1, 2, 21, and 23).

The basic difference between the arrangement of the Trionychinae determined from shell versus skull data is the combination of the Asian and North American clades to the exclusion of the Indian clade in the shell arrangement and the combination of the Indian, North American, and parts of the Asian clades to the exclusion of *Chitra, Pelochelys,* and *Trionyx cartilagineus* in the skull arrangement. These differences are based on very few characters. More importantly, the four major clades which appear in the analyses of all three data sets combined always appear in either the skull or shell arrangement or both. At this point it seems best to consider the evidence for recognition of these four major clades within the Trionychinae. Consideration of a hypothesis about their interrelationship can then follow.

Four groups of species within the Trionychinae are represented as distinct clades or are in close proximity in at least two of the three arrangements based on the three independent data sets and in all most parsimonious arrangements based on united data sets. These are termed the North American clade, the Indian clade, the *Trionyx cartilagineus* clade, and the *T. steindachneri* clade.

The North American clade includes three Old World species, *Trionyx triunguis, T. euphraticus,* and *T. swinhoei,* as well as the three North American forms, *T. ferox, T. muticus,* and *T. spiniferus.* This clade also includes *T. sinensis* in the arrangement based on shell data. All members of this group have eight or fewer neurals (character 14), deeply emarginate prefrontals (character 41), and a large contribution by the parietal to the processus trochlearis oticum (character 78). Except for *T. triunguis,* the members of this clade also have a large foramen intermaxillaris (character 74), second branchial horns which ossify from seven or more centers (character 91), and small to absent eighth pleurals (character 8).

The Indian clade includes *Trionyx gangeticus, T. leithii, T. hurum,* and *T. nigricans.*

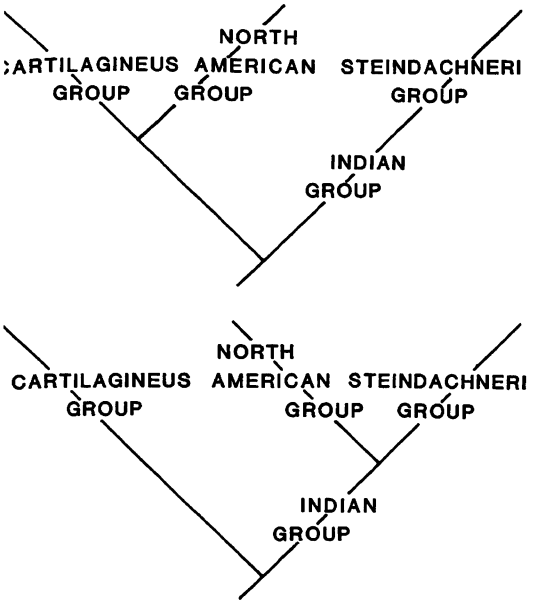

Fig. 30. The two alternative topologies for the ubfamily Trionychinae, each of which appears in hree of six equally parsimonious cladograms of he Trionychidae based on combined skull, shell, nd nonshell postcranial evidence. No supplenentary evidence is available to support one of hese arrangements over the other.

The evidence that this group should be recognized comes entirely from the shell. All our species have a maximum of five plastral allosities, epiplastral extensions of intermediate length, and two neurals between the irst pair of pleurals (characters 4, 9, and 20). The presence of two neurals between the first air of pleurals may be primitive for the Trionychinae but in that case an extra neural nust have been added to the anterior end of he neural series in the common ancestor of ll trionychids. Only one appears between the irst pleurals in carettochelyids, kinosternids, nd dermatemydids. The addition of neural ne in the ancestral trionychid and the subequent fusion of neurals one and two called or in Meylan (1985) are two independent vents. However, the appearance of two eurals between the first pleurals could alernatively be explained by independent vents in the Cyclanorbinae and in the Indian orms of *Trionyx*. In the various arrangenents under consideration here *T. formosus* and some of the members of the *T. steindachneri* group may be included in the Indian clade.

The *Trionyx steindachneri* group appears to include *T. sinensis* and *T. subplanus*. Although these three taxa are not combined in any of the three cladograms based on the three separate data sets, they form a monophyletic group in all six of the equally parsimonious cladograms resulting from analysis of all data combined (figs. 30, 33, 34). The most important character of this group is the unique division of the fenestra postotica by a descending process of the opisthotic in *T. sinensis, T. steindachneri,* and *T. subplanus*. Furthermore, in *T. sinensis* the pterygoid contacts the foramen nervi trigemini anterior to the epipterygoid, unlike the condition in the members of the North American clade in which the contact is posterior to the epipterygoid (see discussion of character 70). *T. sinensis* also lacks the high number of ossifications in the cornu branchiale II, the significant contribution of the parietal to the processus trochlearis oticum, the large foramen intermaxillaris, and the secondarily enlarged vomer found in all members of the North American clade (characters 91, 78, 74, 48, and 49). Recognition of a clade consisting of *T. sinensis, T. steindachneri,* and *T. subplanus* requires that the highly variable neural formula with the last reversal in neural orientation occurring at neural six (characters 15 and 17) and the reappearance of callosities on all plastral elements (character 9) occur independently in *T. sinensis* and in the North American clade. However, reversal of reduction in the eighth peripheral and of sexual size dimorphism which are required in the shell arrangement are not required if *T. sinensis* is withdrawn from the North American clade.

The last of the four groups of species within the Trionychinae includes *Trionyx cartilagineus, Chitra indica,* and *Pelochelys bibroni*. These three species have the foramen posterius canalis carotici interni lying within, rather than below, the lateral crest of the tuberculum basioccipitale, a condition seen elsewhere only in the single available skull of *T. nigricans* (character 60). The epipterygoid frequently contacts the prootic anterior to the foramen nervi trigemini (character 70), and

the eighth cervical vertebra has a distinct ventral ridge (character 87) in all three. Furthermore, these taxa all have a hyoid with eight elements in the corpus hyoidis which occurs elsewhere only in *T. subplanus* and in three species of the North American clade. The highly derived nature of *Chitra* and *Pelochelys* is suggested by their many shared derived features and the unique features of *Chitra.*

The shell characters that conflict with the nonshell evidence for monophyly of these three taxa are relatively minor. An extra posterior neural may appear at times in *Chitra indica* and *Trionyx cartilagineus* and neural reversal may occur one neural more posteriorly in some cases (characters 14 and 17). The clearest conflict in character distribution is the presence of elongate anterior epiplastral projections (character 20) in *T. cartilagineus* and in the Indian and *T. steindachneri* groups. Recognition of these groups requires that elongate epiplastra arise independently on three occasions.

The resolution of the species of the Trionychinae into four clades seems clear and it results in the recognition of groups which other authors have recognized and even named in the past. To finish the task of determining the best hypothesis for relationships among all members of this subfamily, it is necessary to identify the interrelationships of these four clades. Unfortunately, there are few characters which contribute to the understanding of the relationship of these clades to one another and several alternative hypotheses are possible.

Based on the presence of a symphyseal ridge (character 95) (which is absent in species with a short symphysis or reduced overall size) and a constricted basisphenoid (character 64), all of the Indian and Asian forms could be the sister group of the North American clade (fig. 31). Within this Indian and Asian clade, the *Trionyx cartilagineus* group stands out as being highly derived. A sister group to the *T. cartilagineus* group could be defined on two features of the skull: contact of the jugal and squamosal across the quadratojugal (character 32) and contact of jugal and parietal on the skull surface (character 34). These characters occur in some individuals of nearly every species in the Indian clade and in *T. sinensis.* Only the latter character is present in *T. steindachneri* and *T. subplanus,* but the distribution of other characters suggests that the absence of the former is best considered as a reversal.

This arrangement (fig. 31) is the most parsimonious one that will preserve the four species groups as monophyletic units. It is four steps longer than the two shortest trees based on analysis of the skull, shell, mandible, and nonshell postcrania combined.

The two alternative arrangements of the Trionychinae based on the analysis of the combined data sets differ only in the placement of the four trionychine clades (figs. 30, 33, 34). In both, the Indian species group is paraphyletic and the only difference is that the North American forms are the sister group to the *Trionyx cartilagineus* group on the one hand, and to the *T. steindachneri* group on the other. No supplementary evidence is available to support one of these arrangements over the other. Consequently, until additional data can be collected and analyzed, the arrangements shown in figures 33 and 34 must be considered equally plausible, most parsimonious hypotheses for the interfamilial relationships of the Trionychidae. The revised classification which follows reflects the uncertainties which remain in our understanding of trionychid relationships (fig. 32).

Comparison of Results to the Prevailing Hypotheses of Trionychid Relationships

Although there is extensive literature on the taxonomy of soft-shelled turtles, few authors have considered the systematic relationships of all of the family members. The few exceptions are Hummel (1929), Loveridge and Williams (1957), and De Broin (1977). Of these, the Loveridge and Williams treatment gives the most complete consideration of intrafamilial relationships.

These three major systematic studies all recognize at least three of the five species groups thought to represent monophyletic (or paraphyletic) clades in the current study. The Cyclanorbinae and the Indian and North American groups retain their identity in all three. The uniqueness of the genera *Peloche-*

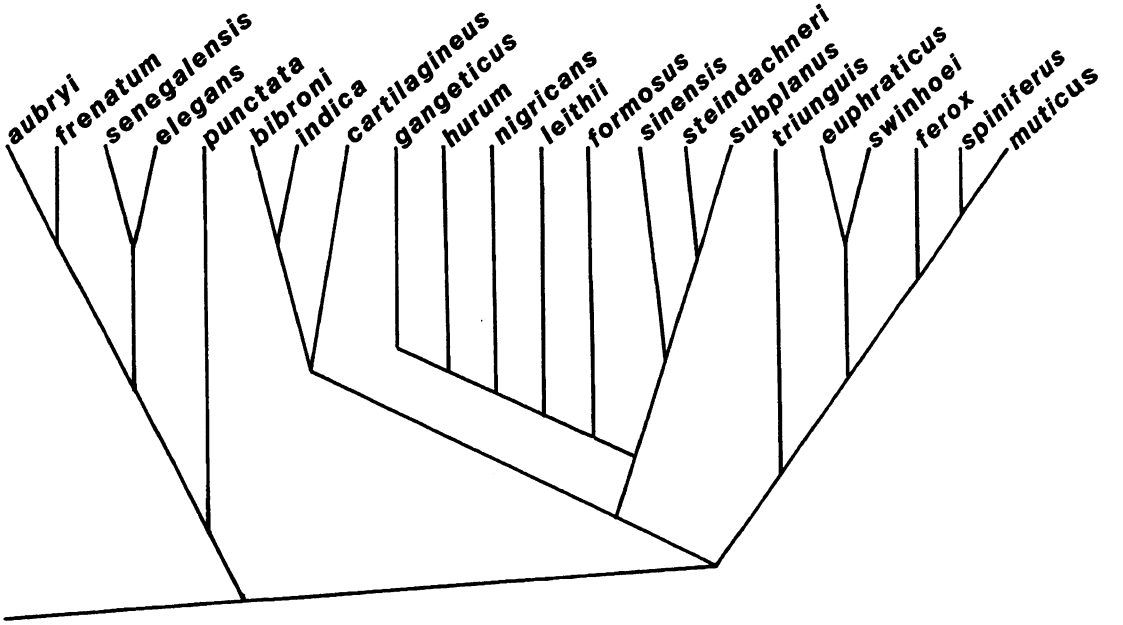

Fig. 31. The topology of the most parsimonious cladogram that preserves monophyly of all four trionychine clades identified during this study. This arrangement is four steps longer that those shown in figures 33 and 34.

lys and *Chitra* is recognized in each, as is the possible relationship of *Trionyx sinensis* to *T. steindachneri.*

Since the time of Boulenger (1889) and Lydekker (1889), soft-shelled turtles that hide their hind feet with flaps of skin have been recognized to be unique relative to other soft-shelled turtles. Only De Broin (1977) questioned the monophyletic nature of this subfamily. The 12 shared, derived features of this subfamily (figs. 33, 34) strongly support its continued recognition. Furthermore, the nine derived features of the Trionychinae indicate monophyly for the remaining trionychids which have previously been placed together without attention to their unique common ancestry.

Loveridge and Williams (1957) detailed the relationships of the African members of the Cyclanorbinae in terms of a progression of what they considered to be the most primitive form, *Cyclanorbis elegans,* to the most derived form, *Cycloderma aubryi,* based on three skull characters. The arrangement of the Cyclanorbinae given in their figure 50 (reproduced here as a cladogram in fig. 1) is identical to one of three alternatives for the Cyclanorbinae derived here (fig. 29A) but not chosen as the best solution. However, they supported monophyly of *Cyclanorbis* and *Cycloderma,* as is suggested by the data considered in the current study.

The Indian clade is recognized in all three previous systematic studies of the family. It has been based in part on the presence of a preneural although this may be primitive for the family. Hay (1904) proposed the name *Aspideretes* for those fossil and Recent trionychine species with a preneural. Hummel (1929) endorsed the use of this term as a subgenus, and De Broin (1977) recognized it alternatively as a valid genus or subgenus. In spite of its apparent paraphyletic nature, recognition of this distinctive taxon may best promote a more complete understanding of trionychine relationships.

De Broin (1977) and Loveridge and Williams (1957) found *Trionyx formosus* and *T. cartilagineus* to be closely related to the Indian clade. The results of this study suggest that *T. formosus* is the sister group of the four Indian species (but that it does not share the features of *Aspideretes*). *T. cartilagineus* is thought to share a unique common ancestor with *Chitra* and *Pelochelys.*

In past studies the North American clade

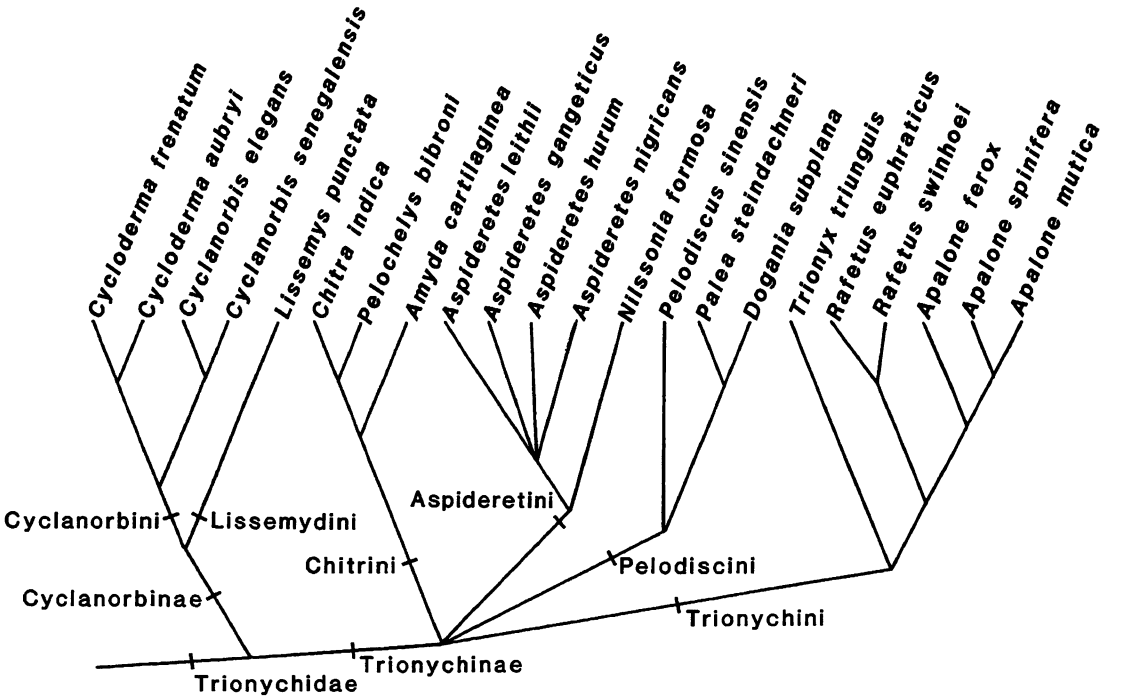

Fig. 32. A cladogram of trionychid relationships derived from the classification supported by this study. The use of a single branch point for the four tribes within the Trionychinae reflects uncertainty about the interrelationships of these four monophyletic groups.

is as frequently recognized as the Indian clade. The present analyses suggest that it includes *Trionyx triunguis, T. euphraticus, T. swinhoei,* and the three living North American species, *T. muticus, T. spiniferus,* and *T. ferox.* No previous study has included *T. triunguis* in this group. Loveridge and Williams (1957) placed *T. triunguis* in a sister group to the North American clade along with *T. sinensis* and *T. steindachneri* (fig. 1). These three species are united only because they each fail to share features of the distinctive groups which these authors recognized. De Broin (1977) considered *T. triunguis* as the remnant of a group that evolved independently from that which led to the North American forms. Based on the osteological features considered here, *T. triunguis* is best considered the sister group of the remainder of the North American clade. The remainder of this clade is recognized in the three previous systematic works and the name *Platypeltis* Fitzinger 1835 was applied to it by Hummel (1929). De Broin (1977) would restrict the use of the name *Platypeltis* to the three North American forms and resurrect the name *Rafetus* Gray 1864 for *T. swinhoei* and *T. euphraticus.* Although *Rafetus* Gray could be applied to these two Old World members of this clade, *Apalone* Rafinesque 1832 (*Trionyx spiniferus* LeSeuer 1827 type species) has priority over *Platypeltis* Fitzinger 1835 and would have to be applied to the three North American forms.

Fortunately, the systematic position of *Trionyx triunguis* is clear. It can stand alone in the arrangement of the family as described above. This is important taxonomically because it is the type species of *Trionyx.* The long muzzle of this species makes it phenetically distinct and the separation of the exoccipital from the pterygoid by the basisphenoid (character 63) is unique and makes it cladistically recognizable.

In past considerations of trionychid relationships the species *Trionyx sinensis* and *T. steindachneri* appear to have been left over after other more distinctive taxa had been

extracted from the Trionychinae. Loveridge and Williams (1957) mentioned the unique feature shared by these two taxa (and also *T. subplanus*), division of the fenestra postotica by a ventral process of the opisthotic, but they do not make full use of this unique quality. In addition to this skull character, these two species and *T. subplanus* share characters of reduced total size and an extremely short nuchal bone. Smith and Smith (1980) indicated that the generic name *Amyda* Geoffroy has *Trionyx cartilagineus* as its type species and thus cannot be applied to this clade as has been suggested by De Broin (1977) and Hummel (1929). The first available name is *Pelodiscus* Gray 1844 for which *T. sinensis* is the type species.

The last of the four trionychine clades recognized in the current study includes *Pelochelys, Chitra,* and *Trionyx cartilagineus.* More than 100 years ago Gray (1873a) recognized a unique relationship between *Chitra* and *Pelochelys* by making them the only members of his subfamily Chitraina of the family Chitridae. Although no authors have followed this arrangement, none have disputed it.

The sister group relationship of *Trionyx cartilagineus* to *Chitra* and *Pelochelys* proposed here is novel. But based on a unique location of the foramen posterior canalis carotici interni (character 60), frequent contact of the epipterygoid and prootic anterior to the foramen nervi trigemini (character 71), absence of contact of epipterygoid and palatine (character 68), and the presence of a fine ridge on the centrum of the eighth cervical vertebra (character 87), the sister relationship of *T. cartilagineus* to these unique genera is well supported. Recognition of the *T. cartilagineus* clade as a single genus seems undesirable given the established quality of the names *Pelochelys* and *Chitra.* But *T. cartilagineus* deserves distinction from the rest of the genus *Trionyx.* In this case the generic name *Amyda* Geoffroy, for which *Testudo cartilaginea* Boddaert (1770) is the type species, should be applied to *T. cartilagineus* (Smith and Smith, 1980).

In summary, the clades recognized by phylogenetic analysis are in nearly every case not totally novel. All have had generic or subgeneric names applied to them. The unique qualities of these clades are not currently conveyed by the broad use of the name *Trionyx* but could be by the use of the available generic names as in the classification which follows (summarized in table 22). If more com-

TABLE 22
Summary of Classification of the Trionychidae Suggested by This Study

Trionychidae (Fitzinger, 1826) Bell, 1828
- Cyclanorbinae Hummel, 1929
  - Cyclanorbini (Hummel, 1929), New Rank
    - *Cyclanorbis* Gray, 1854
      - *Cyclanorbis senegalensis* (Dumeril and Bibron, 1835)
      - *Cyclanorbis elegans* (Gray, 1869)
    - *Cycloderma* Peters, 1854
      - *Cycloderma aubryi* (A. Dumeril, 1856)
      - *Cycloderma frenatum* Peters, 1854
  - Lissemydini (Williams, 1950) New Rank
    - *Lissemys* Malcom Smith, 1931
      - *Lissemys punctata* (Lacépède, 1788)
- Trionychinae (Fitzinger, 1826) Lydekker, 1889
  - Chitrini (Gray, 1870) New Rank
    - *Chitra* Gray, 1844
      - *Chitra indica* (Gray, 1831)
    - *Pelochelys* Gray, 1864
      - *Pelochleys bibroni* (Owen, 1853)
    - *Amyda* Geoffroy, 1809
      - *Amyda cartilaginea* (Boddaert, 1770)
  - Aspideretini, New Tribe
    - *Aspideretes* Hay, 1904
      - *Aspideretes gangeticus* (Cuvier, 1825)
      - *Aspideretes hurum* (Gray, 1831)
      - *Aspideretes leithii* (Gray, 1872)
      - *Aspideretes nigricans* (Anderson, 1875)
    - *Nilssonia* Gray, 1872
      - *Nilssonia formosa* (Gray, 1869)
  - Trionychini (Fitzinger, 1826) New Rank
    - *Trionyx* Geoffroy, 1809
      - *Trionyx triunguis* (Forskäl, 1775)
    - *Rafetus* Gray, 1864
      - *Rafetus euphraticus* (Daudin, 1802)
      - *Rafetus swinhoei* (Gray, 1873)
    - *Apalone* Rafinesque, 1832
      - *Apalone ferox* (Schneider, 1783)
      - *Apalone spinifera* (Le Sueur, 1827)
      - *Apalone mutica* (Le Sueur, 1827)
  - Pelodiscini, New Tribe
    - *Pelodiscus* Gray, 1844
      - *Pelodiscus sinensis* (Wiegmann, 1835)
    - *Dogania* Gray, 1844
      - *Dogania subplana* (Geoffroy, 1809)
    - *Palea,* New Genus
      - *Palea steindachneri* (Siebenrock, 1906)

plete resolution of the interrelationships of the four identified trionychine clades can be achieved, further increase in information content of trionychid classification could result from the use of supertribes to contain tribes of unique common ancestry.

Trends and Mechanisms in Soft-Shelled Turtle Evolution

Although it is possible to trace the changes in character states during the course of evolution of trionychids, many possibilities exist that might explain why these changes have occurred. Three adaptive scenarios could explain portions of the unique morphology of trionychids: (1) selection for greater snapping ability (Pritchard, 1984); (2) selection for high-speed swimming (Pritchard, 1984; personal obs.); and (3) selection for greater aquatic fossoriality (Pritchard, 1984; Bramble, personal commun.).

The apparently critical evolutionary step which allows the unique loss of peripherals in trionychids occurs in carettochelyids. This is the very tight and broad suturing of the rib heads to the vertebral centra. The development of massive rib heads provides a structural alternative to the use of the plastron (via the peripherals) as a tension member (Richmond 1964; Bramble, personal commun.). The peripherals are not strongly sutured to the pleurals in *Carettochelys* and it is unlikely that the plastron is as effective a tension member in this genus as it is in turtles with solid pleuroperipheral and bridge contacts.

The absence of peripherals can most easily be explained by developmental truncation. In the embryonic turtle, ossification centers in the disc margin (those which result in the peripherals, nuchal, and pygal bones) are the last to form (Zangerl, 1969). Consequently, the trionychid shell may be paedomorphic; that is, the final step in carapace development never occurs.

Paedomorphosis may be the mechanism by which the unique trionychid shell morphology evolved. However, few other features of soft-shelled turtles can be ascribed to a truncation of development. The only characters which might also be a result of paedomorphosis are those of the pubic elements. As noted, the pectineal processes of the pubic bones lie in a single plane as appears to be the case early in ontogeny of other turtles. Furthermore, ossification of the prepubic region, which occurs in most living cryptodires, never occurs in trionychids. The absence of other paedomorphic features of soft-shelled turtle morphology suggests that developmental truncation has not been an overriding influence on the evolution of the group.

The most completely described adaptive hypothesis for the unique shell form of trionychids is that of Pritchard (1984). He suggested that *Chitra* is the best model for the ancestral trionychid, and that the unique body form of trionychids is an adaptation for a rapid predatory strike (one of his three listed adaptations for piscivory). His evidence is partly based on the similarity of the skull of *Chitra* to that of *Chitracephalus dumonii* Dollo 1884 from the Jurassic or Cretaceous of Europe, and partly on his observation that *Chitra* is the most developed piscivore among the trionychids and that other forms have secondarily become more generalized.

Other than their similar skull shape, there is nothing to suggest that *Chitracephalus* is related to the trionychids (Gaffney, 1979b). Pritchard himself stated that the long, narrow skull found in these two forms appears a number of times in turtle evolution. He cites *Glyptops* (a pleurosternid) and *Deirochelys* (an emydid) as examples. The superficial similarity of *Chitracephalus* and *Chitra* goes beyond the overall skull shape: both have large and well-developed hyoids. However, judging from unpublished stereo photographs of the type of *Chitracephalus,* the corpus hyoidis in the type is not composed of multiple ossifications and what appears to be a jugal-quadratojugal bar is actually the lower jaw. Thus, *Chitracephalus* has continuous cheek and temporal emargination which is not known elsewhere among the Cryptodira.

Further arguments against using *Chitra* as the ancestral trionychid can be taken directly from the phylogenetic analyses conducted in this study. The many unique features of *Chitra* (and *Chitra* plus *Pelochelys*) would have to be lost secondarily in all other trionychids. A good example is the extensive postorbital bar. The hypothesis supported by the phylogenetically analyzed data suggests that a very

narrow postorbital bar first allowed contact of the jugal and parietal and that expansion of this contact is secondarily increased in *Chitra* and other species in the family with long, narrow skulls. Other features, including extensive hyperphalangy (Boulenger, 1889), the presence of large dorsal spines on the fifth and sixth cervicals, the narrow symphysis, the very short nuchal bone with the first thoracic vertebra located at the anterior margin, and the unique hyoid with a massive corpus hyoidis of eight ossifications and large second branchial arch of three strongly sutured ossifications, would all have to appear and then be lost in the course of trionychid evolution. It is far more parsimonious to consider the genus *Chitra* as a highly specialized trionychid (with all of its derived features appearing only once). Conversely, Pritchard's (1984) argument that *Lissemys punctata* is the most derived of trionychids remains unsupported. The view that it is the most primitive (Walther, 1922; Deraniyagala, 1939) is corroborated in the current study.

Pritchard (1984) suggested that swimming prowess and aquatic fossoriality are two secondary advantages of modification of shell shape in trionychids. Bramble (personal commun.) has also pointed out that fossorial activity is enhanced by the shape of the trionychid carapace. Certainly, the flattened body form of trionychids provides reduced resistance to motion through water, sand, or mud. It is only after the loss of peripherals in trionychids that there has been a remarkable decrease in the relative proportion of the total carapace made up by the bony disc. A concomitant increase in the flexible margin, which would assist in aquatic fossoriality, also occurs at this stage, indicating that fossoriality may in fact be a secondary result of peripheral loss, and not necessarily the cause for their loss.

Although trionychids have reduced shells, they are found living with turtle-eating crocodilians throughout much of their range. Their survival under such circumstances may be ascribed to crypsis or to their swimming speed. Trionychids may be among the fastest swimming freshwater turtles (see Webb, 1962, and references therein). It has been my observation that *Trionyx ferox* is the fastest swimming turtle that one encounters in clear Florida spring runs. Selection for better swimming ability could explain the acquisition of numerous derived features noted during the course of this study, especially those of the shell and girdles.

Trends toward reduction in shell size, including reduction in the number of peripherals, neurals, and plastral callosities, and reduction in the size of the eighth pleurals and the nuchal bone could all be attempts to lighten the shell, with shell streamlining as the result. Reduction of the bridge is important in allowing maximum retraction of the hind limbs for a maximum power stroke in swimming (Zug, 1971).

Loss of epidermal scutes may also act to reduce the weight of the shell. If Coldiron (1974) is correct in his hypothesis that dermal bone sculpturing acts to disperse stresses on broad areas of dermal bone (crocodilian and labryinthodont skulls), sculpturing could be an alternative shell-strengthening mechanism to epidermal scutes in trionychids.

Acquisition of hyperphalangy can be correlated with increased swimming prowess. Strong contact of the radius and ulna stiffens the forearm and probably produces a better paddle in trionychids, carettochelyids, and cheloniids. The reduction of the transverse processes of the tenth thoracic vertebra that occurs in all trionychoids might increase the capacity of the pelvic girdle to rotate and thus contribute to the very long hind-limb power stroke of trionychids (Zug, 1971). The expanded pectineal processes of the pelvic girdle and the relatively enlarged coracoids both provide additional surface area for muscle attachment. Thus it appears that selection for improved swimming speed would account for many of the derived features noted to occur in the Trionychidae.

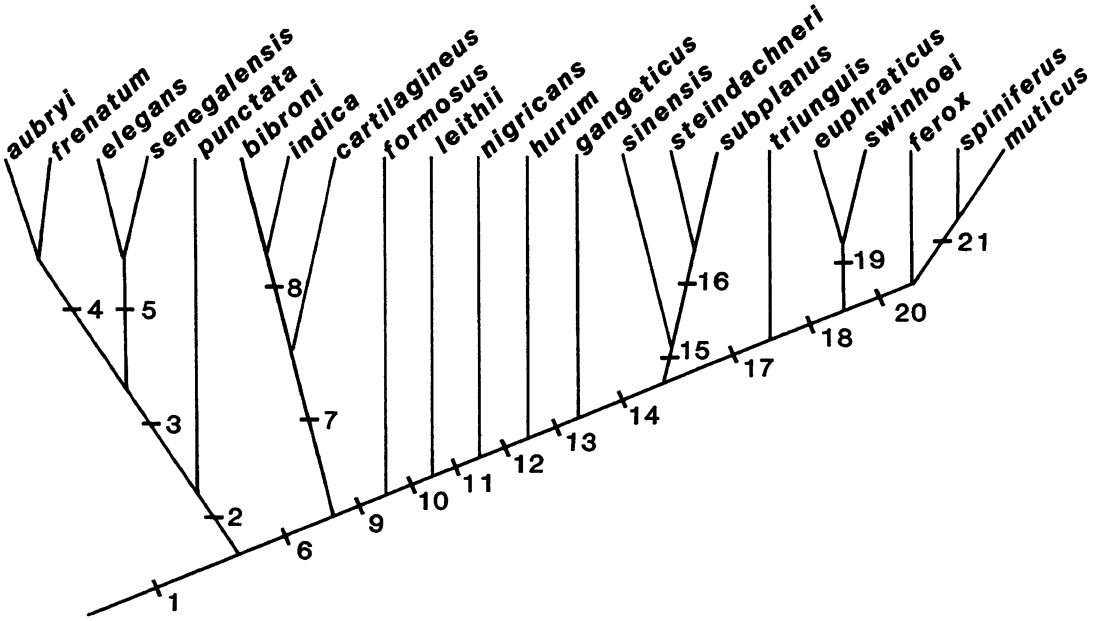

Fig. 33. One of two most parsimonious arrangements of the living Trionychidae. Characters supporting the nodes are as follows: **Node 1:** The evidence for monophyly of the Trionychidae is summarized in table 21. **Node 2:** — 10(2) hyoplastra and hypoplastra fuse just after hatching, — 13(2) hypoplastra are lateral to xiphiplastra at hypo-xiphiplastral union, — 14(2) eight or nine neurals (reduced from always nine) (occurs also at node 19 and in *indica* and *leithii*), — 16(2) eighth pleural only or seventh and eighth pleurals meet on midline (occurs also at node 11), — 17(1) neural reversal always occurs at neural eight (may be primitive condition), — 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 15 and in *leithii* and *muticus*), — 54(2) foramen palatinum posterius forms in palatine only (occurs also in *sinensis* and *swinhoei*), — 58(2) foramen jugulare posterius excluded from fenestra postotica by pterygoid arching to contact opisthotic, — 68(2) epipterygoid excluded from contact with palatine in 50% of cases where it is present (occurs also at node 8), — 93(2) basihyals in close contact and projecting anteriorly, — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 12 and in *indica* and *formosus*), — 107(1) ischia extend into thyroid fenestra (reversal of a derived condition shared by most trionychids, carettochelyids, and staurotypine kinosternids, — 109(2) metischsial processes not well developed (occurs also at node 11). **Node 3:** — 5(4) no peripheral elements (occurs also at node 6), — 34(3) jugal always contacts parietal on skull surface (occurs also at node 8 and in *formosus* and *steindachneri*), — 36(2) vomer not in contact with prefrontal (occurs also in *indica* and reverses in *elegans*), — 53(3) foramina palatinum posterius small and divided, — 69(2) no contact between pterygoid and foramen nervi trigemini when epipterygoid is present (occurs also in *muticus* and *steindachneri*), — 72(2) epipterygoid contacts prootic posterior to foramen nervi trigemini, — 100(2) ilia curve medially, — 113(1) coracoid shorter than either process of scapula (unique among trionychids). **Node 4:** — 19(2) epiplastra I-shaped (occurs also in *punctata*), — 25(2) carapace straight or concave posterolaterally (occurs also in *punctata*), — 53(4) posterior palatine foramen consists of many small foramina, — 68(3) epipterygoid never contacts palatine (occurs also at node 8 and in *nigricans* and *senegalensis*), — 88(2) strong dorsal processes on cervicals (occurs also at node 9). **Node 5:** — 2(2) anterior and posterior costiform processes united (occurs also at node 6), — 3(2) anterior edge of first body vertebra is in the middle of the nuchal bone (occurs also at node 6 and in *aubryi*), — 107(2) no extension of ischia into thyroid fenestra (occurs also at node 6), — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 9 and 14). **Node 6:** — 1(3) nuchal at least three times wider than long (occurs also in *senegalensis*), — 2(2) anterior and posterior costiform processes united (occurs also at node 5), — 3(2) anterior edge of first body vertebra in the middle of the nuchal (occurs also at node 5 and in *aubryi*), — 5(4) no peripheral bones (occurs also at node 3), — 9(3) four plastral

Fig. 33 (*continued*).

callosities (reversal to 5 occurs at node 16 and in *cartilagineus*), — 17(3) neural series reverses at neural six or seven or anterior to that point, — 21(2) depressions for ilia in eighth pleural absent (occurs also in *elegans*), — 23(2) bridge short (occurs also in *elegans*), — 41(2) dorsal edge of apertura narium externum weakly emarginate (occurs also in *aubryi* and *senegalensis*), — 64(2) basisphenoid occasionally medially constricted, — 73(3) epipterygoid never fuses to pterygoid, — 91(2) two or more ossifications in second branchial horn of hyoid, — 95(2) symphyseal ridge strong and present in a depression, — 107(2) no extension of ischia into thyroid fenestra (occurs also at node 5). **Node 7:** — 4(2) first and second neurals fused (occurs also at node 14), — 60(2) foramen posterius canalis carotici interni occurs within lateral crest of basioccipital tubercle (occurs also in *nigricans*), — 70(0) when epipterygoid is present pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all (occurs also at node 17 and in *leithii*), — 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in about 50% of sample (occurs also in *hurum*), — 87(2) ventral keel on eighth cervical present and limited to posterior end of centrum (occurs also at node 19), — 90(3) eight ossifications make up corpus hyoidis (occurs also at node 18 and in *hurum* and *subplanus*). **Node 8:** — 9(3) four callosities present in plastron (occurs also at node 14 and in *formosus*), — 17(3) reversal of neural orientation occurs at neural six or seven (occurs also at node 10), — 34(3) jugal always contacts parietal on skull surface (also occurs at node 3 and in *formosus* and *steindachneri*), — 41(1) dorsal edge of apertura narium externum not emarginate (a reversal that occurs elsewhere only in *frenatum*), — 48(1) vomer divides maxillae (a presumed reversal that occurs at node 18 and in *senegalensis*), — 49(1) vomer reaches intermaxillary foramen (a presumed reversal that occurs also at node 18 and in *punctata* and *senegalensis*), — 64(1) basisphenoid not medially constricted (occurs also at node 17), — 68(3) epipterygoid never contacts palatine (occurs also at node 4 and in *nigricans* and *senegalensis*), — 88(2) strong dorsal processes present on cervicals five and six (occurs also at node 4), — 92(2) ossifications of second branchial horn broad and strongly sutured, — 95(1) no symphyseal ridge (occurs also at node 14), — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 3 and 21). **Node 9:** — 32(2) jugal contacts squamosal in one-half of sample (occurs also in *muticus, sinensis,* and *swinhoei*), — 64(3) basisphenoid medially constricted, — 68(1) epipterygoid always contacts palatine when present (a reversal that occurs also in *elegans*). **Node 10:** — 17(3) point of reversal of neural orientation at neural six or seven (occurs also at node 8), — 20(2) anterior extension of epiplastra is intermediate. **Node 11:** — 16(2) pleurals seven and eight or eight only meet on midline (occurs also at node 2), — 34(1) jugal never contacts parietal on skull surface (a reversal that occurs also in *cartilagineus*). **Node 12:** — 15(2) neural reversal occurs at one of two adjacent neurals, — 32(1) jugal never contacts squamosal (a reversal), — 41(3) dorsal edge of apertura narium externum strongly laterally emarginate. **Node 13:** — 14(2) some individuals with only eight (rather than nine) neurals (fused one and two counted as two) (occurs also at node 2 and in *bibroni* and *leithii*), — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also in *cartilagineus, elegans,* and *frenatum*). **Node 14:** — 4(2) first and second neurals fused (occurs also at node 7), — 9(3) four callosities present in plastron (occurs also at node 8 and in *formosus*), — 95(1) symphyseal ridge absent (occurs also at node 8). **Node 15:** — 1(4) width of nuchal bone more than four times length (occurs also in *muticus*), — 20(3) anterior extension of epiplastra is long (occurs also in *cartilagineus*), — 24(2) largest adult size 200 mm or less (occurs also at node 21), — 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 2 and in *hurum* and *muticus*), — 59(2) foramen jugulare posterius excluded from fenestra postotica by descending process of opisthotic which reaches pterygoid, — 70(2) when epipterygoid is present, pterygoid contacts foramen nervi trigemini between epipterygoid and parietal or not at all. **Node 16:** — 17(2) neural reversal occurs at neural seven (a reversal), — 69(2) no contact occurs between pterygoid and foramen nervi trigemini when epipterygoid is present (occurs also at nodes 3 and 21). **Node 17:** — 14(3) eight neurals, — 15(1) neural reversal always occurs at same neural (a reversal that occurs also in *steindachneri*), — 20(1) anterior extension of epiplastra short (a reversal), — 64(1) basisphenoid not medially constricted (a reversal that occurs also at node 8), — 70(0) when epipterygoid is present, pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all (occurs also at node 7 and in *leithii*), — 78(2) 22.1% or more of processus trochlearis oticum is made up by parietal (occurs also in *elegans* and *nigricans*). **Node 18:** — 8(2) eighth pleurals reduced or absent, — 48(1) vomer divides maxillae (a reversal that occurs also at node 8 and in *senegalensis*), — 49(1) vomer reaches intermaxillary foramen (a reversal that occurs also at node 8 and in *punctata* and *senegalensis*). — 74(2) average ratio of intermaxillary foramen length to length primary palate about 0.60, — 90(3)

Fig. 33 (*continued*).

eight ossifications in corpus hyoidis (occurs also at node 7), — 91(3) seven or more ossifications in second branchial horn (occurs also in *gangeticus*), — 109(2) metischial process not distinct (occurs also at node 2). **Node 19:** — 9(4) two callosities on plastron (occurs also in *elegans*), — 41(2) dorsal edge of apertura narium externum weakly laterally emarginate (a reversal that occurs also in *gangeticus*), — 87(2) weak ventral keel present on posterior end of eighth cervical (occurs also at node 7), — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2 and in *formosus* and *indica*). **Node 20:** — 15(3) position of reversal of neural orientation highly variable, often two reversals present (occurs also in *sinensis*), — 17(4) point of reversal of neural orientation at neural six, — 29(2) sexual dimorphism in disc length. **Node 21:** — 9(1) seven callosities in plastron of large adults (a reversal that occurs also in *sinensis*), — 24(2) largest adult disc length 200 mm or less (occurs also at node 15), — 69(2) contact between pterygoid and foramen nervi trigemini is absent when epipterygoid is present (occurs also at nodes 3 and 16), — 75(2) postorbital bar less than one-fifth of orbit diameter (occurs also at node 16), — 90(2) six ossifications in corpus hyoidis (a reversal), — 109(1) metischial processes present and distinct (a reversal), — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 3 and 8). Specific characters. *aubryi:* — 3(2) anterior edge of first body vertebra at middle of nuchal (occurs also at nodes 5 and 6), — 12(2) xiphiplastra may fuse on midline (occurs also in *punctata*), — 65(2) premaxillae occasionally absent (occurs also in *punctata*), — 68(2) epipterygoid, if present, fails to contact palatine in one-half of sample (a reversal). *frenatum:* — 3(1) anterior edge of first body vertebra lies at posterior edge of nuchal (a reversal that occurs also in *punctata*), — 17(2) reversal of neural orientation occurs at neural seven (occurs also at node 16), — 41(1) dorsal margin of apertura narium externum is not emarginate (a reversal that occurs also at node 8), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, elegans, gangeticus, muticus, subplanus,* and *triunguis*), — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at node 13 and in *cartilagineus* and *frenatum*). *elegans,* — 9(4) two plastral callosities (occurs also at node 19), — 21(2) no depressions for ilia on eighth pleurals (occurs also at node 6), — 23(2) bridge short (occurs also at node 6), — 68(1) epipterygoid contacts palatine when present (occurs also at node 9), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, frenatum, gangeticus, muticus, subplanus,* and *triunguis*), — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at node 13 and in *cartilagineus* and *frenatum*), — 78(2) 22.1% or more of processus trochlearis oticum made up by parietal (occurs also at node 17 and in *nigricans*). *senegalensis:* — 1(3) nuchal more than three times wider than long (occurs also at node 6), — 7(2) prenuchal bone present (occurs also in *punctata*), — 9(0) nine callosities in plastron, — 14(5) seven or fewer neurals, — 16(4) pleurals in addition to numbers six, seven, and eight meet at midline, — 48(1) vomer divides maxillae (occurs also at nodes 8 and 18), — 49(1) vomer reaches intermaxillary foramen (occurs also at nodes 8 and 18 and in *punctata*), — 68(3) when present epipterygoid does not contact palatine (occurs also at nodes 4 and 8 and in *nigricans*). *punctata:* — 7(2) prenuchal bone present (occurs also in *senegalensis*), — 12(2) xiphiplastra fuse in large adults (occurs also in *aubryi*), — 14(4) seven or eight neurals, — 19(2) epiplastra I-shaped (occurs also at node 4), — 25(2) carapace straight or concave posterolaterally (occurs also at node 4), — 49(1) vomer reaches intermaxillary foramen (occurs also at nodes 8 and 18 and in *senegalensis*), — 65(2) premaxilla occasionally absent (occurs also in *aubryi,* frequently absent in *indica*). *bibroni:* — 14(2) eight or nine neurals (occurs also at nodes 2 and 13 and in *leithii*), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *elegans, frenatum, gangeticus, muticus, subplanus,* and *triunguis*). *indica:* — 3(3) anterior edge of first body vertebra at anterior edge of nuchal, — 29(2) sexual dimorphism in disc length, — 36(2) vomer does not contact prefrontals (occurs also at node 3), — 65(3) premaxillae usually absent, — 71(3) epipterygoid contacts prootic anterior to foramen nervi trigemini (occurs also in *steindachneri*), — 74(0) intermaxillary foramen about 7% of primary palate length, — 75(0) postorbital bar about two times orbit width, — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 2 and 19 and in *formosus*). *cartilagineus:* — 20(3) long anterior projections of epiplastra (occurs also at node 15), — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at node 13 and in *elegans, frenatum,* and *steindachneri*). *formosus:* — 1(2) nuchal between two and three times wider than long (a reversal that occurs elsewhere in *steindachneri*), — 9(3) four callosities in plastron (occurs also at nodes 8 and 14), — 34(3) jugal always contacts parietal on skull surface (also occurs at nodes 3 and 8 and in *steindachneri*), — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 2 and 19 and in *indica*). *leithii:* — 14(2) eight or nine neurals (occurs also at nodes 2 and 13 and in *bibroni* and *muticus*), — 70(0) when epipterygoid is present, pterygoid contacts

Fig. 33 (*continued*).
foramen nervi trigemini between epipterygoid and quadrate or not at all (occurs also at nodes 7 and 17). *nigricans:* — 60(2) foramen posterius canalis carotici interni occurs within lateral crest of basioccipital tubercle (occurs also at node 7), — 68(3) when present epipterygoid does not contact palatine (occurs also at nodes 4 and 8 and in *senegalensis*), — 78(2) 22.1% or more of processus trochlearis oticum made up by parietal (occurs also at node 17 and in *elegans*). *hurum:* — 34(2) jugal contacts parietal in one-half of sample (occurs also at nodes 2 and 15 and in *muticus*), — 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in about one-half of sample (occurs also at node 7), — 90(3) eight ossifications in corpus hyoidis (occurs also at nodes 7 and 18 and in *subplanus*), — 91(1) only one ossification in second branchial horn (a unique reversal). *gangeticus:* — 41(2) dorsolateral edge of apertura narium externum weakly emarginate (a reversal that occurs also at node 19), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, elegans, frenatum, muticus, subplanus,* and *triunguis*), — 91(3) seven or more ossifications in second branchial horn (occurs also at node 18). *sinensis:* — 9(1) seven plastral callosities present in plastron (a reversal that occurs also at node 21), — 15(3) position of neural reversal highly variable with more than one reversal sometimes present (occurs also at node 20), — 17(4) posteriormost neural reversal present at neural six or anterior (occurs also at node 20), — 32(2) jugal contacts squamosal in one-half of sample (occurs also in *formosus, leithii, nigricans, muticus,* and *swinhoei*), — 54(2) foramen palatinum posterius forms in palatine only (occurs also at node 2 and in *swinhoei*). *steindachneri:* — 1(2) nuchal between two and three times wider than long (a reversal that occurs elsewhere in *formosus*), — 15(1) position of neural reversal is always at the same neural (a reversal that occurs also at node 17), — 34(3) jugal always contacts parietal on skull surface (also occurs at nodes 3 and 8 and in *formosus*), — 71(3) epipterygoid always contacts prootic anterior to foramen nervi trigemini (occurs also in *indica*), — 76(1) quadratojugal not participating in processus trochlearis oticum (a unique reversal). *subplanus:* — 14(1) nine neurals present (a unique reversal), — 16(0) no pleurals meeting at midline, — 64(2) basisphenoid occasionally medially constricted (a unique reversal), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, elegans, frenatum, gangeticus, muticus,* and *triunguis*), — 90(3) eight ossifications in corpus hyoidis (occurs also at nodes 7 and 18 and in *hurum*), — 95(2) symphyseal ridge present and in a depression (occurs after loss at node 14). *triunguis:* 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, elegans, frenatum, gangeticus, muticus,* and *subplanus*). *euphraticus:* — 46(1) basisphenoid fails to reach palatines (unique among trionychids), — 64(2) basisphenoid occasionally medially constricted (a reappearance after loss at node 17). *swinhoei:* — 32(2) jugal contacts squamosal in one-half of sample (occurs also in *formosus, leithii, nigricans, muticus,* and *sinensis*), — 54(2) foramen palatinum posterius forms in palatine only (occurs also at node 2 and in *sinensis*). *ferox:* — 11(2) hyoplastra and hypoplastra fuse in adults. *spiniferus:* — 64(2) basisphenoid occasionally medially constricted. *muticus:* — 1(4) nuchal bone more than four times wider than long (occurs also at node 15), — 14(2) eight or nine neurals (occurs also at nodes 2 and 13 and in *bibroni* and *leithii*), — 32(2) jugal contacts squamosal in one-half of sample (occurs also in *formosus, leithii, nigricans, muticus,* and *swinhoei*), — 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 2 and 15 and in *hurum*), — 49(2) vomer fails to reach intermaxillary foramen (a unique reversal), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, elegans, frenatum, gangeticus, subplanus,* and *triunguis*), — 91(2) two or more ossifications in second branchial horn of hyoid.

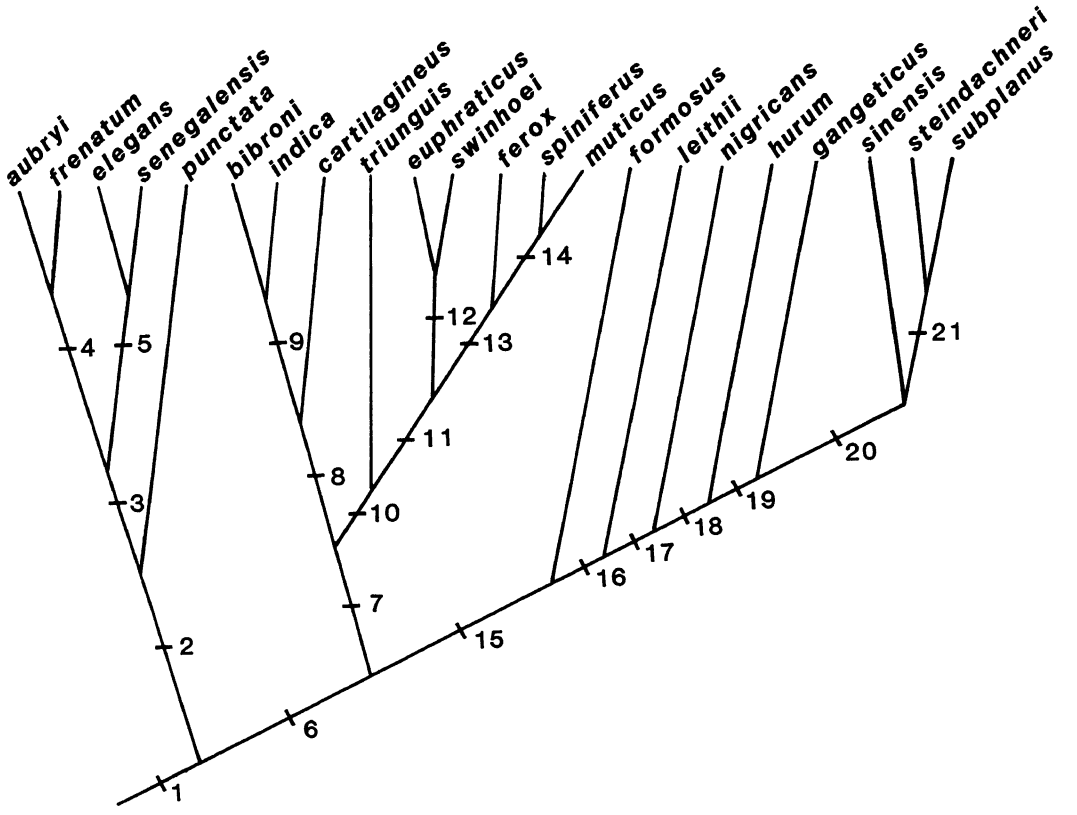

Fig. 34. The second of two most parsimonious cladograms of the living Trionychidae. Characters supporting the nodes are as follows: **Node 1:** The evidence for monophyly of the Trionychidae is summarized in table 21. **Node 2:** — 10(2) hyoplastra and hypoplastra fuse just after hatching, — 13(2) hypoplastra are lateral to xiphiplastra at hypoxiphiplastral union, — 14(2) eight or nine neurals (reduced from always nine) (occurs also at node 19 and in *indica* and *leithii*), — 16(2) eighth pleurals only or seventh and eighth pleurals meet on midline (occurs also at nodes 10 and 17), — 17(1) neural reversal always occurs at neural eight (may be primitive condition), — 54(2) foramen palatinum posterius forms in palatine only (occurs also in *sinensis* and *swinhoei*), — 58(2) foramen jugulare posterius excluded from fenestra postotica by pterygoid arching to contact opisthotic, — 68(2) epipterygoid excluded from contact with palatine in 50 percent of cases where it is present (occurs also at node 8), — 93(2) basihyals in close contact and projecting anteriorly, — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 12 and in *indica* and *formosus*), — 107(1) ischia extend into thyroid fenestra (reversal of a derived condition shared by most trionychids, carettochelyids, and staurotypine kinosternids), — 109(2) metischial processes not well developed (occurs also at node 11). **Node 3:** — 5(4) no peripheral elements (occurs also at node 6), — 34(3) jugal always contacts parietal on skull surface (occurs also in *formosus, indica,* and *steindachneri*), — 36(2) vomer not in contact with prefrontal (occurs also in *indica* and reverses in *elegans*), — 53(3) foramina palatinum posterius small and divided, — 69(2) no contact between pterygoid and foramen nervi trigemini when epipterygoid is present (occurs also in *muticus* and *steindachneri*), — 72(2) epipterygoid contacts prootic posterior to foramen nervi trigemini, — 100(2) ilia curve medially, — 113(1) coracoid shorter than either process of scapula (unique among trionychids). **Node 4:** — 19(2) epiplastra I-shaped (occurs also in *punctata*), — 25(2) carapace straight or concave posterolaterally (occurs also in *punctata*), — 53(4) posterior palatine foramen consists of many small foramina, — 88(2) strong dorsal processes on cervicals (occurs also at node 9). **Node 5:** — 2(2) anterior and posterior costiform processes united (occurs also at node 6), — 3(2) anterior edge of first body vertebra is in the middle of the nuchal bone (occurs also at node

Fig. 34 (*continued*).

6 and in *aubryi*), — 107(2) no extension of ischia into thyroid fenestra (occurs also at node 6), — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 9 and 14). **Node 6:** — 1(3) nuchal at least three times wider than long (occurs also in *senegalensis*), — 2(2) anterior and posterior costiform processes united (occurs also at node 5), — 3(2) anterior edge of first body vertebra in the middle of the nuchal (occurs also at node 5 and in *aubryi*), — 5(4) no peripheral bones (occurs also at node 3), — 9(3) four plastral callosities (reversal to 5 occurs at node 16 and in *cartilagineus*), — 17(3) orientation of neural series reverses at neural six or seven or anterior to that point, — 21(2) depressions for ilia in eighth pleural absent (occurs also in *elegans*), — 23(2) bridge short (occurs also in *elegans*), — 41(2) dorsal edge of apertura narium externum weakly emarginate (occurs also in *aubryi* and *senegalensis*), — 73(3) epipterygoid never fuses to pterygoid, — 91(2) two or more ossifications in second branchial horn of hyoid, — 107(2) no extension of ischia into thyroid fenestra (occurs also at node 5). **Node 7:** — 4(2) first and second neurals fuse (occurs also at node 20), — 34(1) jugal never contacts parietal on skull surface (a reversal), — 70(0) when epipterygoid is present, pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all, — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also in *elegans, frenatum, gangeticus,* and *sinensis*), — 90(3) eight ossifications in corpus hyoideum. **Node 8:** — 60(2) foramen posterius canalis carotici interni lies within ridges which extend laterally from the basioccipital tubercles (occurs also in *nigricans*), — 68(2) when present, epipterygoid fails to contact palatine in 50 percent or more of sample (occurs also at node 2 and in *nigricans*), — 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in 50 percent or more of sample (occurs also in *hurum* and *steindachneri*), — 87(2) a ventral keel present on posterior end of 8th cervical (occurs also in *euphraticus*). **Node 9:** — 34(3) jugal always contacts parietal on skull surface (also occurs at node 3 in *formosus* and *steindachneri*), — 41(1) no dorsal emargination of apertura narium externum (a unique reversal), — 48(1) vomer divides maxillae (occurs also at node 11 and in *senegalensis*), — 49(1) vomer reaches intermaxillary foramen (occurs also at node 11, in *punctata* and in *senegalensis*), — 68(3) when present, epipterygoid never contacts palatine (occurs also in *frenatum, nigricans,* and *senegalensis*), — 76(1) no contribution by quadratojugal to processus trochlearis oticum (a reversal that occurs elsewhere in *steindachneri*), — 88(2) strong dorsal processes on cervicals (occurs also at node 4), — 92(2) ossifications of second branchial horn broad and strongly sutured, — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion. **Node 10:** — 14(3) eight or fewer neurals (fused one and two counted as two), — 16(2) seventh and eighth pleurals meet in some individuals (occurs also at node 2 and at node 17), — 41(3) dorsal edge of apertura narium externum strongly emarginate (occurs also at node 18), — 78(2) parietal makes up 22.1 percent or more of processus trochlearis oticum (occurs also in *elegans* and *nigricans*). **Node 11:** — 8(2) eighth pleurals reduced or absent, — 48(1) vomer divides maxillae (occurs also at node 9 and in *senegalensis*), — 49(1) vomer reaches foramen intermaxillaris (occurs also at node 9, in *senegalensis* and *punctata*), — 74(2) intermaxillary foramen about 60% of length of primary palate, — 91(3) seven or more ossifications in second branchial horn (also occurs in *gangeticus*), — 109(2) no distinct metischial processes (occurs also at node 2). **Node 12:** — 9(4) only two callosities on plastron (occurs also in *elegans*), — 41(2) dorsal edge of apertura narium externum weakly emarginate (a unique reversal to a condition widespread in the trionychinae), — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2, in *formosus* and *indica*). **Node 13:** — 15(3) location of neural reversals highly variable (occurs also in *sinensis*), — 17(4) posteriormost reversal occurs at neural six (occurs also in *sinensis*), — 29(2) sexual dimorphism in disc length (occurs also in *indica*). **Node 14:** — 9(1) seven plastral callosities (a reversal to most primitive condition which occurs also in *sinensis*), — 24(2) largest adult size about 200 mm or less disc length (occurs also at node 20), — 69(2) contact between pterygoid and foramen nervi trigemini does not occur when epipterygoid is present (occurs also at node 3 and in *steindachneri*), — 75(2) postorbital bar very narrow, less than one-fifth orbit diameter (occurs also at node 21), — 90(2) six ossifications in corpus hyoidis (a reversal that occurs also in *triunguis*), — 109(1) metischial processes present and distinct (a unique reversal), — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 5 and 9). **Node 15:** — 32(2) jugal contacts squamosal in about one-half of sample (occurs also in *euphraticus, muticus,* and *sinensis*), — 64(3) basisphenoid almost always medially constricted, — 95(2) symphyseal ridge strong and in a depression (occurs also in *cartilagineus*). **Node 16:** — 9(2) five callosities present in plastron (a reversal that occurs also in *cartilagineus*), — 20(2) anterior processes of epiplastra of intermediate length. **Node 17:** — 16(2) seventh and eighth pleurals meet on midline in some individuals (occurs also at nodes

Fig. 34 (*continued*).

2 and 10). **Node 18:** — 15(2) neural reversal occurs at adjacent neurals, — 32(1) jugal never contacts squamosal (a unique reversal). **Node 19:** — 14(2) some individuals with eight neurals (fused first and second neurals counted as two, occurs also at node 2, and in *bibroni*), — 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at node 7, and in *elegans* and *frenatum*). **Node 20:** — 1(4) nuchal bone four or more times wider than long (occurs also in *muticus*), — 4(2) first and second neurals fused (occurs also at node 7), — 20(3) anterior processes of epiplastra long (occurs also in *cartilagineus*), — 24(2) largest adult size about 200 mm disc length (occurs also at node 14), — 59(2) foramen jugulare posterius excluded from fenestra postotica by descending process of opisthotic which usually reaches pterygoid, — 70(2) when epipterygoid is present pterygoid contacts foramen nervi trigemini between epipterygoid and parietal or not at all. **Node 21:** — 9(3) four plastral callosities (a reversal to the common condition in trionychines), — 17(2) posteriormost neural reversal occurs at neural seven or anterior to it (a reversal that occurs also in *cartilagineus* and *formosus*), — 75(2) postorbital bar less than one-fifth of orbit diameter (occurs also at node 14). Specific characters. *aubryi:* — 3(2) anterior edge of first body vertebra at middle of nuchal bone (occurs also at nodes 5 and 6), — 12(2) xiphiplastra fuse in some individuals (occurs also in some *punctata*), — 41(2) dorsal edge of apertura narium externum weakly emarginate (occurs also at node 6 and in *senegalensis*), — 65(2) premaxillae usually absent. *frenatum:* — 68(3) epipterygoid, when present, never contacts palatine (occurs also at node 9, in *nigricans* and in *senegalensis*), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *elegans, bibroni, triunguis, muticus, gangeticus,* and *subplanus*). *elegans:* — 9(4) only two plastral callosities (occurs also at node 12), — 21(2) depressions on eighth pleurals for contact of ilia absent (occurs also at node 6), — 23(2) bridge short (occurs also at node 6), — 36(1) vomer contacts prefrontal (a unique reversal), — 42(2) dorsal edge of apertura narium externum medially emarginate, — 68(1) when present, epipterygoid always contacts palatine (a unique reversal), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *frenatum, bibroni, triunguis, muticus, gangeticus,* and *subplanus*), — 100(1) ilia do not curve medially (a unique reversal). *senegalensis:* — 1(3) nuchal three times wider than long (occurs also at node 6), — 7(2) prenuchal bone present (occurs also in *punctata*), — 9(0) nine or more plastral callosities (includes gular pair), — 14(5) seven or fewer neurals, — 16(4) pleural bones, in addition to pairs six, seven, and eight, meet at the midline, — 41(2) dorsal edge of apertura narium externum weakly emarginate laterally (occurs also at node 6 and in *aubryi*), — 48(1) vomer divides maxillae (occurs also at nodes 9 and 11), — 49(1) vomer reaches intermaxillary foramen (occurs also at nodes 9 and 11 and in *punctata*), — 68(3) when present, epipterygoid never contacts palatine. *punctata:* — 7(2) prenuchal bone present (occurs also in *senegalensis*), — 12(2) xiphiplastra fuse in some individuals (occurs also in some *aubryi*), — 14(4) some individuals with seven neurals in continuous series, — 19(2) epiplastra I-shaped (occurs also at node 4), — 25(2) carapace straight or concave laterally (occurs also at node 4), — 49(1) vomer reaches intermaxillary foramen (occurs also at nodes 9 and 11 and in *senegalensis*). *bibroni:* — 14(2) some individuals with eight (rather than nine) neurals (occurs also at nodes 2 and 19 and in *leithii*), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *frenatum, elegans, triunguis, muticus, gangeticus,* and *subplanus*). *indica:* — 3(3) anterior edge of first body vertebra at anterior edge of nuchal bone, — 29(2) sexual dimorphism in disc length (occurs also at node 13), — 36(2) vomer fails to contact prefrontal (occurs also at node 3), — 65(3) premaxilla usually absent (occurs also in *aubryi*), — 71(3) epipterygoid always contacts prootic anterior to foramen nervi trigemini (occurs also in *steindachneri*), — 74(0) intermaxillary foramen quite reduced, averaging 7% of primary palate, — 75(0) postorbital bar about two times orbit diameter, — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 12 and in *formosus*). *cartilagineus:* — 9(2) five plastral callosities (a reversal that occurs also at node 18), — 17(2) posteriormost neural reversal occurs at neural seven (a character reversal that occurs also at node 21 and in *formosus*), — 20(3) anterior epiplastral process long (occurs also at node 20), — 64(2) basisphenoid occasionally medially constricted (occurs also in *euphraticus* and *spiniferus*), — 95(2) strong symphyseal ridge present (occurs also at node 15). *triunguis:* — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, frenatum, elegans, muticus, gangeticus,* and *subplanus*), — 90(2) six ossifications in corpus hyoidis (a reversal that occurs also at node 14). *euphraticus:* — 64(2) basisphenoid occasionally medially constricted (occurs also in *cartilagineus* and *spiniferus*), — 87(2) ventral keel present on posterior end of eighth cervical (occurs also at node 8). *swinhoei:* — 32(2) jugal contacts squamosal in one-half of sample (occurs also at node 15 and in *muticus* and *sinensis*), — 54(2) foramen palatinum posterius forms in palatine only (occurs also at node 2). *ferox:* — 11(2) hyo- and hypoplastra fuse in adults. *spiniferus:* — 64(2) basisphenoid me-

Fig. 34 (*continued*).

dially constricted on occasion (occurs also in *cartilagineus, euphraticus* and *subplanus*). *muticus:* — 1(4) nuchal bone four or more times wider than long (occurs also at node 20), — 32(2) jugal contacts squamosal in one-half of sample (occurs also at node 15 and in *swinhoei* and *sinensis*), — 34(2) jugal contacts parietal on skull surface in one-half of sample (unique occurrence after reversal at node 7), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, frenatum, elegans, gangeticus, subplanus,* and *triunguis*), — 91(2) between two and six ossifications in second branchial horn of hyoid (a unique reversal). *formosus:* — 1(2) nuchal bone only two times wider than long (a reversal that occurs also in *steindachneri*), — 17(2) last reversal in neural orientation occurs at neural seven (a character reversal that occurs also at node 21 and in *cartilagineus*), — 34(3) jugal always contacts parietal on skull surface (also occurs at nodes 3 and 9 and in *steindachneri*), — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 12 and in *indica*). *leithii:* — 14(2) some individuals with eight neurals (occurs also at nodes 2 and 19 and in *bibroni*), — 70(0) when epipterygoid is present pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all (occurs also at node 7). *nigricans:* — 34(1) jugal never contacts parietal on skull surface (a reversal that occurs at node 7 and in *gangeticus*), — 60(2) foramen posterius canalis carotici interni located within a lateral crest of the basioccipital tubercle (occurs also at node 8), — 68(3) epipterygoid does not contact palatine (occurs also at node 9 and in *frenatum* and *senegalensis*), — 78(2) parietal makes up 22.1% or more of processus trochlearis oticum. *hurum:* — 41(3) dorsal edge of apertura narium externum strongly emarginate laterally (occurs also at nodes 10 and 20), — 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in one-half of sample, — 90(3) eight ossifications in corpus hyoidis (occurs also at node 7 and in *subplanus*), — 91(1) a single ossification in the second horn of hyoid (a unique reversal). *gangeticus:* — 34(1) jugal never contacts parietal on skull surface (a reversal that occurs at node 7 and in *nigricans*), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, frenatum, elegans, muticus, triunguis,* and *subplanus*), — 91(3) seven or more ossifications in second branchial horn of hyoid (occurs also at node 11). *sinensis:* — 9(1) seven callosities in plastron (a reversal that occurs also at node 14), — 15(3) high variability of point of posteriormost neural reversal (occurs also at node 13), — 17(4) posteriormost neural reversal occurs at or anterior to neural six (occurs also at node 13), — 32(2) jugal contacts squamosal in one-half of sample (occurs also at node 15 and in *muticus* and *swinhoei*), — 54(2) foramen palatinum posterius forms in palatine only (occurs also at node 2), — 95(1) symphyseal ridge absent (a reversal that occurs also in *steindachneri*). *steindachneri:* — 1(2) nuchal bone only two times wider than long (a reversal that occurs also in *formosus*), — 15(1) neural reversal always occurs at the same neural (a unique reversal), — 34(3) jugal always contacts parietal on skull surface (also occurs at nodes 3 and 9 and in *formosus*), — 71(3) epipterygoid contacts prootic anterior to foramen nervi trigemini (occurs also in *indica*), — 76(1) quadratojugal excluded from processus trochlearis oticum (a reversal that occurs also at node 9), — 95(1) symphyseal ridge absent (a reversal that occurs also in *sinensis*). *subplanus:* — 14(1) nine neurals present (a unique reversal), — 16(0) no pleurals meet on midline, — 64(2) basisphenoid medially constricted on occasion (occurs also in *cartilagineus, euphraticus,* and *spiniferus*), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in *bibroni, frenatum, elegans, muticus, triunguis,* and *gangeticus*), — 90(3) eight ossifications in corpus hyoidis (occurs also at node 7 and in *hurum*).

CLASSIFICATION OF THE LIVING TRIONYCHIDAE

TRIONYCHIDAE (FITZINGER, 1826; AS TRIONYCHOIDEA) BELL, 1828

TYPE GENUS: *Trionyx* Geoffroy, 1809.

DIAGNOSIS: Members of the Trionychoidea (sensu Gaffney, 1975, 1984) with 18 or fewer peripherals, no pygal or suprapygal, a boomerang-shaped entoplastron, quadratojugal not contacting postorbital, jugal contacting parietal, premaxillae fused and excluded from apertura narium externum by maxillae, hyperphalangy of manus digits four and five and pes digit four, three clawed digits in manus and pes, cervical centra all opisthocoelous except eighth which lacks central articulation to first thoracic vertebra, no ventral process of eighth cervical vertebra, corpus hyoidis composed of six or eight ossifications, ilia curve posteriorly, pectineal processes lie in a single plane and are in broad contact with plastron, and pectineal processes equal to or wider than interpubic contact.

CONTENT: Twenty-two living species divided among two subfamilies (the Cyclanorbinae and Trionychinae) and about 220 named fossil species, some of which are, on occasion, placed in a third subfamily, the Plastomeninae.

SUBFAMILY CYCLANORBINAE HUMMEL, 1929

TYPE GENUS: *Cyclanorbis* Gray, 1854.

DIAGNOSIS: Trionychid turtles in which the hyo- and hypoplastra fuse just after hatching, the hypoplastra are lateral to the xiphiplastra at the hypoxiphiplastral union, the basihyals of the corpus hyoidis are in close contact and project anteriorly, the foramen intermandibularis caudalis is never enclosed by the prearticular, metischial processes are not well developed, foramen palatinum posterius forms within the palatine, and the foramen jugulare posterius is isolated from the fenestra postotica by dorsal arch of the pterygoid.

CONTENT: Considered to include five living species here divided into two tribes.

TRIBE CYCLANORBINI (HUMMEL, 1929; AS CYCLANORBINAE) NEW RANK

TYPE GENUS: *Cyclanorbis* Gray, 1854.

DIAGNOSIS: Members of Cyclanorbinae having no peripheral elements, medially curving ilia, coracoid shorter than either process of scapula, jugal always in contact with parietal on dorsal surface of skull, vomer not in contact with prefrontal (except in *Cyclanorbis elegans*), foramen palatinum posterius small and divided, no contact between pterygoid and foramen nervi trigemini when epipterygoid is present, and epipterygoid-prootic contact posterior to foramen nervi trigemini.

CONTENT: The four living species of this tribe belong to two genera, *Cyclanorbis* and *Cycloderma.*

Cyclanorbis Gray, 1854

TYPE SPECIES: *Cyclanorbis senegalensis* (Dumeril and Bibron, 1835).

DIAGNOSIS: Cyclanorbine trionychids, with the anterior and posterior costiform processes united, no extension of ischia into thyroid fenestra, angle between acromion process and body of scapula approaching that of acromion to coracoid, and a variable tendency of pleurals to divide the neural series by meeting on the midline.

CONTENT: Two species, *Cyclanorbis senegalensis* and *Cyclanorbis elegans.*

Cyclanorbis senegalensis (Dumeril and Bibron, 1835)

DIAGNOSIS: A species of *Cyclanorbis* with a prenuchal bone present, nine or more plastral callosities, seven or fewer neural bones, pleural bones in addition to numbers six, seven, and eight meeting on the midline, vomer dividing maxillae and reaching intermaxillary foramen, and epipterygoid never contacting palatine.

Cyclanorbis elegans (Gray, 1869)

DIAGNOSIS: A species of *Cyclanorbis* with only two plastral callosities, no depressions on the eighth pleurals for articulation of ilia, a short bridge, the vomer in contact with the prefrontals; when present, epipterygoid always in contact with palatine, and apertura narium externum medially emarginate.

Cycloderma Peters, 1854

TYPE SPECIES: *Cycloderma frenatum* Peters, 1854.

DIAGNOSIS: Members of Cyclanorbini in which the epiplastra are I-shaped rather than J-shaped, the margin of the carapace is concave posterolaterally, the middle cervicals (4, 5, and 6) possess well-developed dorsal processes, and the posterior palatine foramina consist of numerous very small openings barely distinguishable from the nutritive foramina of the palate.

CONTENT: Two living species, *Cycloderma frenatum* and *Cycloderma aubryi.*

Cycloderma frenatum Peters, 1854

DIAGNOSIS: Members of *Cycloderma* in which the epipterygoid, when present, never contacts the palatine and fuses to the pterygoid in large adults, and in which the vomer is absent.

This species differs further from its living congener in retaining primitive features including the total absence of midline suturing or fusion of the xiphiplastra and in always retaining the premaxillae.

Cycloderma aubryi (A. Duméril, 1856)

DIAGNOSIS: Members of *Cycloderma* in which the xiphiplastra suture and fuse on the midline in large adults, the dorsal edge of the apertura narium externum is weakly emarginate, and premaxillae are usually absent.

TRIBE LISSEMYDINI
(WILLIAMS, 1950; AS LISSEMYDINAE)
NEW RANK

TYPE GENUS: *Lissemys* Malcolm Smith, 1931.

DIAGNOSIS: Cyclanorbine trionychids with a prenuchal bone, I-shaped epiplastra, posterolaterally concave carapacial margin and in which the xiphiplastra suture and fuse on the midline in large adults and the vomer reaches the intermaxillary foramen dorsal to the maxillae. Members of this tribe differ further from all other known trionychids by the primitive retention of peripheral elements.

CONTENT: One genus *Lissemys* here considered to include a single species *Lissemys punctata.*

Lissemys Malcolm Smith, 1931

TYPE SPECIES: *Lissemys punctata* (Lacépède, 1788).

DIAGNOSIS: As for the tribe Lissemydini.

CONTENT: As for the tribe Lissemydini.

Lissemys punctata (Lacépède, 1788)

DIAGNOSIS: As for the tribe Lissemydini.

SUBFAMILY TRIONYCHINAE
(FITZINGER, 1826; AS TRIONYCHOIDEA)
LYDEKKER, 1889

TYPE GENUS: *Trionyx* Geoffroy, 1809.

DIAGNOSIS: Trionychid turtles with the nuchal bone at least three times wider than long, anterior and posterior costiform processes united, no peripheral bones, neural series always containing at least one reversal of neural orientation, depressions for articulation of ilia absent from eighth pleural, a short bridge, two or more ossifications in the second branchial horn (except in some *hurum*), dorsal edge of apertura narium externum slightly to strongly emarginate, and epipterygoid typically fusing to pterygoid in adults.

CONTENT: This study suggests that the subfamily Trionychinae consists of four monophyletic species groups. However, the relationships between the four groups is not totally resolved. To reflect this lack of resolution the recognition of four tribes is recommended below. By failing to designate groups between the rank of subfamily and tribe, the uncertainty about the interrelationships of these tribes can be indicated. In the interest of maintaining as much nomenclatorial stability as possible, the use of four tribes at this level is thought to be preferable to the recognition of four genera. The four tribes constituting the Trionychinae are the

Chitrini, Aspideretini, Trionychini, and Pelodiscini.

TRIBE CHITRINI
(GRAY, 1870; AS CHITRADAE)
NEW RANK

TYPE GENUS: *Chitra* Gray, 1844.

DIAGNOSIS: Trionychine trionychids in which the foramen posterius canalis carotici interni lies within a ridge extending laterally from the basioccipital tubercle, the eighth cervical has a small ventral keel, and the epipterygoid usually does not contact the palatine but usually does contact the prootic anterior to the foramen nervi trigemini.

CONTENT: In the interest of nomenclatorial stability this tribe is herein considered to be composed of three monotypic genera in two subtribes: *Chitra indica, Pelochelys bibroni,* and *Amyda cartilaginea.*

SUBTRIBE CHITRINA
(GRAY, 1870; AS CHITRADAE)
NEW RANK

TYPE GENUS: *Chitra* Gray, 1844.

DIAGNOSIS: Members of the tribe Chitrini with strong dorsal processes on cervicals four, five, and six, ossifications of the second branchial horn of the hyoid composed of three wide elements which are strongly sutured to one another, jugal always in contact with parietal on skull surface, no dorsal emargination of apertura narium externum, and vomer dividing maxillae and reaching intermaxillary foramen.

CONTENT: Contains *Pelochelys bibroni* and *Chitra indica* and is used to suggest that they share a common ancestor not shared by *Amyda cartilaginea.*

Chitra Gray, 1844

TYPE SPECIES: *Chitra indica* (Gray, 1831).

DIAGNOSIS: Members of the subtribe Chitrina in which the anterior edge of the prezygapophysis of the first thoracic vertebra lies at the anterior edge of the carapace, the foramen intermandibularis caudalis is never enclosed by the prearticular, the intermaxillary foramen is quite reduced (about 7% of primary palate), the postorbital bar is two times orbit diameter, the premaxillary is usually absent, and sexual dimorphism may exist (Wirot, 1979).

CONTENT: The only living form is *Chitra indica.*

Chitra indica (Gray, 1831)

DIAGNOSIS: As for the genus.

Pelochelys Gray, 1864

TYPE SPECIES: *Pelochelys bibroni* (Owen, 1853).

DIAGNOSIS: Members of the subtribe Chitrina which sometimes have eight neurals (rather than nine, with fused one and two counted as two), vomer often contacts basisphenoid, and the epipterygoids fuse to the pterygoid in adults.

Pelochelys differs further from its living sister taxon, *Chitra indica,* in retaining primitive features including: prezygapophyses of the first thoracic vertebra recessed below the nuchal, foramen intermandibularis caudalis sometimes enclosed by prearticular, intermaxillary foramen larger (about 37% of primary palate), postorbital bar two-thirds of the width of the orbit, premaxillary usually present, and sexual dimorphism unknown.

SUBTRIBE AMYDINA
(LOVERIDGE, 1942; AS AMYDIDAE)
NEW RANK

TYPE GENUS: *Amyda* Geoffroy, 1809.

DIAGNOSIS: Members of the tribe Chitrini with five plastral callosities, elongate anterior projections of epiplastra, a long symphysis with a strong symphyseal ridge, and frequently a medially constricted basisphenoid.

CONTENT: The only living member is *Amyda cartilaginea.*

Amyda Geoffroy, 1809

TYPE SPECIES: *Amyda cartilaginea* (Boddaert, 1770).

DIAGNOSIS: As for the subtribe Amydina.

CONTENT: As for the subtribe Amydina.

Amyda cartilaginea (Boddaert, 1770)

DIAGNOSIS: As for the subtribe Amydina.

TRIBE TRIONYCHINI (FITZINGER, 1826; AS TRIONYCHOIDEA) NEW RANK

TYPE GENUS: *Trionyx* Geoffroy, 1809.

DIAGNOSIS: Members of the subfamily Trionychinae with eight or fewer neurals (fused first and second count as two), parietal makes up nearly one-quarter of processus trochlearis oticum, and dorsal margin of apertura narium externum is strongly emarginate (except in *swinhoei* and *euphraticus*).

CONTENT: Considered to include six living species: *triunguis, euphraticus, swinhoei, ferox, spiniferus,* and *muticus.* The relationships within this tribe, as understood from the current analysis, can best be portrayed through the use of two subtribes, three genera, and two subgenera.

SUBTRIBE TRIONYCHINA (FITZINGER, 1826; AS TRIONYCHOIDEA) NEW RANK

TYPE GENUS: *Trionyx* Geoffroy, 1809.

DIAGNOSIS: Members of Trionychini with six ossifications in the corpus hyoidis, epipterygoid fusing to the pterygoid in very large adults, and exoccipital partly or completely isolated from the pterygoid by the basioccipital. Differing further from members of the sister subtribe in its primitive retention of complete eighth pleurals and a smaller intermaxillary foramen (about one-third primary palate).

CONTENT: One species, *Trionyx triunguis.*

Genus *Trionyx* Geoffroy, 1809

TYPE SPECIES: *Trionyx triunguis* (Forskäl, 1775).

DIAGNOSIS: As for subtribe Trionychina.

CONTENT: As for subtribe Trionychina.

Trionyx triunguis (Forskäl, 1775)

DIAGNOSIS: As for subtribe Trionychina.

SUBTRIBE APALONINA NEW NAME

TYPE GENUS: *Apalone* Rafinesque, 1832.

DIAGNOSIS: Members of the Tribe Trionychini in which the eighth pair of pleurals is reduced or absent, there are seven or more ossifications in the second branchial horn, the intermaxillary foramen is about 60 percent of primary palate in length, there is no distinct metischial process (except in *spiniferus* and *muticus*), and the vomer divides the maxillae and reaches the intermaxillary foramen.

CONTENT: The relationships of the members of this subtribe can be completely portrayed by the use of two generic names, *Rafetus* and *Apalone,* with two subgenera (*Platypeltis* and *Apalone*) constituting the latter.

Rafetus Gray, 1864

TYPE SPECIES: *Rafetus euphraticus* (Daudin, 1802).

DIAGNOSIS: Members of the subtribe Apalonina with only two callosities in the plastron, the foramen intermandibularis caudalis never enclosed by the prearticular, and the dorsal edge of the apertura narium externum only weakly emarginate.

CONTENT: Two living species, *euphraticus* and *swinhoei.*

Rafetus euphraticus (Daudin, 1802)

DIAGNOSIS: Members of the genus *Rafetus* with a ventral keel present on the eighth cervical vertebra, the basisphenoid medially constricted in some individuals, and the basisphenoid failing to contact the palatines.

Rafetus swinhoei (Gray, 1873)

DIAGNOSIS: Members of the genus *Rafetus* in which the jugal contacts the squamosal, the foramen palatinum posterius is surrounded by the palatine, and the basisphenoid contacts the palatines.

Apalone Rafinesque, 1832

TYPE SPECIES: *Apalone spiniferus* (Le Sueur, 1827).

DIAGNOSIS: Members of the subtribe Apalonina in which the location of the posteriormost neural reversal is highly variable but occurs at or anterior to neural six and in which there is marked sexual dimorphism.

CONTENT: Two subgenera, *Apalone* and *Platypeltis* are used within this genus to reflect the relationship of the three included species.

Apalone (*Apalone*) *spinifera*
(Le Sueur, 1827)

DIAGNOSIS: Members of the genus *Apalone* that can be distinguished from congeners belonging to the subgenus *Platypeltis* by the presence of seven plastral callosities in old adult males, small adult size (200 mm or less disc length), six ossifications in corpus hyoidis, postorbital bar about one-fifth orbit diameter, metischial process distinct, angle of acromion to scapula approaches that of coracoid to acromion, and contact between pterygoid and foramen nervi trigemini does not occur when epipterygoid is present. This species can be distinguished from its sister taxon, *Apalone* (*Apalone*) *muticus,* by its higher number of ossifications in the second branchial horn (seven or more), its medially constricted basisphenoid (occurs only in some individuals), and by relatively primitive conditions for nuchal shape (about three times wider than long) and jugal contacts (never contacts parietal on skull surface).

Apalone (*Apalone*) *mutica*
Le Sueur, 1827

DIAGNOSIS: Members of the genus *Apalone* that can be distinguished from congeners belonging to the subgenus *Platypeltis* by the presence of seven plastral callosities in old adult males, small adult size (200 mm or less disc length), six ossifications in corpus hyoidis, postorbital bar about one-fifth of orbit diameter, metischial processes distinct, angle of acromion to scapula approaches that of coracoid to acromion, and contact between pterygoid and foramen nervi trigemini does not occur when epipterygoid is present. This species can be distinguished from its sister taxon *Apalone* (*Apalone*) *spinifera* by its wider nuchal bone (four times wider than long), jugal which contacts parietal on skull surface and/or with squamosal in some individuals, and six or fewer ossifications in the second branchial horn of the hyoid.

Apalone (*Platypeltis*) *ferox*
(Schneider, 1783)

DIAGNOSIS: Members of the genus *Apalone* which can most easily be distinguished from members of the sister taxon (subgenus *Apalone*) by the fusion of the hyo-hypoplastra which occurs in nearly all adults. This species is further diagnosable by only four callosities in the plastron of all adult individuals, eight ossifications in the adult corpus hyoidis, absence of metischial processes, wider acromion to scapula angle, and large adult size.

TRIBE ASPIDERETINI, NEW NAME

TYPE GENUS: *Aspideretes* Hay, 1904.

DIAGNOSIS: Trionychine turtles with the basisphenoid medially constricted, a strong symphyseal ridge in a depression, the quadrate excluded from the foramen nervi trigemini by contact of the pterygoid and prootic posterior to this structure (except in *A. leithii*), and jugal contacting squamosal in some individuals.

CONTENT: Here considered to include two genera, *Aspideretes* and *Nilssonia.*

Aspideretes Hay, 1904

TYPE SPECIES: *Aspideretes gangeticus* (Cuvier, 1825).

DIAGNOSIS: Members of Aspideritini most easily recognized by two pairs of neurals between the first pair of pleurals, five callosities in the plastron, and anterior epiplastral projections of intermediate length.

CONTENT: The interrelationships of the four living species in this genus is not fully resolved. To reflect this no superspecific ranks are used within the genus. The genus contains four living species: *gangeticus, hurum, leithii,* and *nigricans.*

Aspideretes gangeticus (Cuvier, 1825)

DIAGNOSIS: A species of the genus *Aspideretes* with seven or more ossifications in the second branchial horn of the hyoid, jugal never contacting parietal on skull surface, and quadratojugal participating in processus trochlearis oticum.

Aspideretes hurum (Gray, 1831)

DIAGNOSIS: A species of *Aspideretes* with only one ossification in the second branchial horn, eight ossifications in the corpus hyoi-

dis, the dorsal margin of the apertura narium externum strongly emarginate, and the epipterygoid (when present) contacting the prootic in front of the foramen nervi trigemini in some individuals.

Aspideretes leithii (Gray, 1872)

DIAGNOSIS: Members of *Aspideretes* in which some individuals have eight rather than nine neurals and in which the pterygoid, if contacting the foramen nervi trigemini, does so between the epipterygoid (when present) and the quadrate. Further diagnosed by primitive conditions for those specialized features which are diagnostic for its congeners.

Aspideretes nigricans (Anderson, 1875)

DIAGNOSIS: Members of *Aspideretes* in which the jugal never contacts the parietal on the skull surface (true also of *gangeticus*), the foramen posterior canalis carotici interni is located within a crest extending anterolaterally from the basioccipital tubercle, the parietal makes up more than 22 percent of the processus trochlearis oticum, and the epipterygoid is not known to contact the palatine.

Nilssonia Gray, 1872

TYPE SPECIES: *Nilssonia formosa* (Gray, 1869).

DIAGNOSIS: Members of Aspideretini with a single neural (fused one and two) between the first pair of pleurals, the nuchal bone only two times wider than long, the last neural reversal occurring at neural seven, the jugal always in contact with the parietal on the skull surface, and the foramen intermandibularis caudalis never enclosed by the prearticular.

CONTENT: The single living species *Nilssonia formosa.*

Nilssonia formosa (Gray, 1869)

DIAGNOSIS: As for the genus *Nilssonia.*

TRIBE PELODISCINI, NEW NAME

TYPE GENUS: *Pelodiscus* Gray, 1844.

DIAGNOSIS: Trionychine turtles in which the epiplastra are significantly anteriorly extended (more than 40% of hyohypoplastron width), the largest adult size is 200 mm or less (with one possible exception), the foramen jugulare posterius is excluded completely or partially from the fenestra postotica by a descending process of the opisthotic, and when the pterygoid contacts the foramen nervi trigemini it does so between the epipterygoid (when present) and the parietal.

CONTENT: In order to completely portray relationships and to encourage use of the name *Dogania* for the highly derived species *subplana,* this tribe is considered to be composed of two subtribes and three monotypic genera.

SUBTRIBE PELODISCINA, NEW NAME

TYPE GENUS: *Pelodiscus* Gray, 1844.

DIAGNOSIS: Members of Pelodiscini with seven callosities in the adult plastron, location of the last neural reversal highly variable but always occurring at or anterior to neural six, jugal contacting squamosal in some individuals, and foramen palatinum posterius surrounded by the palatine.

CONTENT: Contains only *Pelodiscus sinensis.*

Pelodiscus Gray, 1844

TYPE SPECIES: *Pelodiscus sinensis* (Weigmann, 1835).

DIAGNOSIS: Same as for subtribe Pelodiscina.

CONTENT: Same as for subtribe Pelodiscina.

Pelodiscus sinensis Weigmann, 1835

DIAGNOSIS: Same as for subtribe Pelodiscina.

SUBTRIBE DOGANIINA, NEW NAME

TYPE GENUS: *Dogania.*

DIAGNOSIS: Members of the tribe Pelodiscini with four plastral callosities, posteriormost neural reversal occurring as far posterior as neural seven, long anterior processes of the epiplastra, and postorbital bar less than one-fifth of orbit diameter.

CONTENT: Two monotypic genera, *Dogania* and *Palea.*

Dogania Gray, 1844

TYPE SPECIES: *Dogania subplana* (Geoffroy, 1809).

DIAGNOSIS: Members of the subtribe Doganiina with a complete series of nine neurals (first and second fused) which divide all of the pleurals along the midline, eight ossifications in the corpus hyoidis, basisphenoid often medially constricted, postorbital bar one-ninth of orbit diameter, and maxillae contacting frontals along anterior margin of orbits.

CONTENT: Contains only *Dogania subplana.*

Dogania subplana (Geoffroy, 1809)

DIAGNOSIS: Same as for genus *Dogania.*

***Palea*, new genus**

TYPE SPECIES: *Palea steindachneri* (Siebenrock, 1906).

DIAGNOSIS: Members of the subtribe Doganiina with the nuchal bone only two times wider than long, neural reversal always occurring at the same neural (number 7), jugal always contacting parietal on skull surface, and epipterygoid contacting prootic anterior to the foramen nervi trigemini.

ETYMOLOGY: From the Latin *palea,* meaning wattles, in reference to the autapomorphic structures on the neck.

CONTENT: Contains only *Palea steindachneri* (Siebenrock, 1906).

Palea steindachneri (Siebenrock, 1906)

DIAGNOSIS: Same as for genus *Palea.*

ACKNOWLEDGMENTS

The progress of this study has relied on a great number of people and to all of them I extend my thanks. My doctoral committee, Walter Auffenberg, David Webb, Jon Reiskind and Doug Jones has been supportive and encouraging throughout the course of this study. I have benefited from numerous discussions of turtle systematics and phylogeny with my colleagues, Dennis Bramble, Chuck Crumly, Jim Dobie, Ren Hirayama, Howard Hutchison, John Iverson, Peter Pritchard, and especially Gene Gaffney. This contribution has been improved through the efforts of Gene Gaffney, Howard Hutchison, John Iverson, Sam McDowell, Hobart Smith, Bob Webb, and Barbara Werschek all of whom have read part or all of the manuscript critically.

For loans and/or access to museum collections I am grateful to the following curators and collection managers: C. W. Myers and staff, American Museum of Natural History (AMNH); Jim Dobie, Auburn University Museum of Paleontology (AUMP); Nick Arnold, Colin McCarthy, and Barry Clarke, British Museum of Natural History (BMNH); Harold Voris, Field Museum of Natural History (FMNH); J. P. Gosse, Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB); Richard Leakey and Alec Duff-McKay, Kenya National Museum (KNM); Pere Alberch and Jose Rosado, Museum of Comparative Zoology, Harvard (MCZ); E. R. Brygoo, Roger Bour, and J. P. Gasc, Museum National d'Histoire Naturelle, Paris (MNHNP); D. F. E. Thys van den Audenaerde, Musee Royal de l'Afrique Central, Tervuren (MRAC); U. Rahm, Naturhistorisches Museum, Basel (NHMB); J. L. Perret, Museum d'Histoire Naturelle, Geneva (NHMG); Franz Tiedemann and Heinz Grillitsch, Naturhistorisches Museum, Vienna (NMW); Don Broadley, National Museum of Zimbabwe (NMZB); M. S. Hoogmoed, Rijksmuseum van Natuurlijke Historie (RMNH); K. Klemmer, Natur-Museum Senkenberg, Frankfurt (SMF); Walter Auffenberg and Dave Auth, Florida State Museum (UF); Arnold Kluge and Dennis Harris, Museum of Zoology, University of Michigan (UMMZ); George Zug, United States National Museum (USNM); and Ulrich Gruber and Dieter Fuchs, Zoologisches Sammlung der Bayerisches Staates, Munich (ZSM). For access to specimens in their private collections I thank

John Iverson (JBI and JI), Ed Moll (EOM), Peter Pritchard (PCHP), Richard Etheridge (RE), and Ren Hirayama (RH).

Vince DeMarco made the histological preparations. Frank Ipollito prepared figures 4, 5, 6, 8, 14E, 17, 18, 19, 20, and 21. Ian Brehney prepared figure 9. All or part of figures 10, 11, 12, 14, 15, and 16 were made available by Gene Gaffney. Chester Tarka, Lorraine Meeker, Carol Gelber, and Bill Weinstein provided technical assistance.

This study has been supported by a grant from the Leakey Foundation, by Colonel Barkau, by the Department of Zoology and the Florida State Museum, University of Florida, and by the Department of Vertebrate Paleontology and the James Walter Carter Memorial Fund of the American Museum of Natural History. To the staff of the Florida State Museum I give special thanks for support of many kinds.

For Anne there are never thanks enough.

Appendix 1. Specimens Examined

The modal conditions of characters for members of the Trionychidae listed in tables 3, 11, and 17 are based on the following specimens. For specimens with more than one catalog number (BMNH, MNHNP) the earliest number is given. See acknowledgments for explanation of museum acronyms.

Apalone ferox AMNH 129737, PCHP 343, PCHP 354, PCHP 1171, PCHP 1532, PCHP 1533, PCHP 1534, PCHP unnumbered, UF 10963, UF 11124, UF 11126, UF 14270, UF 14363, UF 18932, UF 32999, UF 33434, UF 33436, UF 33447, UF 33453, UF 37545, UF 40534, UF 52886, UF 52887, UF 53172, UF 53173, UF 53174, UF 53175, UF 53382, UF 53383, UF 53568, UF 53569, UF 53570, UF 53671, UF 53672, UF 53673, UF 54212, UF 54547, UF 55576, UF T-1203.

Apalone mutica PCHP 1611, PCHP unnumbered, UF 55789, UF 57724, UF 57725, UF 57729, UMMZ 128086, UMMZ 155231.

Apalone spinifera IRSNB 231, PCHP 1479, PCHP 1480, PCHP unnumbered, UF 22392, UF 37228, UF 40614, UF 43154, UF 43889, UF 45181, UF 45182, UF 45183, UF 45184, UF 45356, UF 48257, UF 50811, UF 51093, UF 51094, UF 55564.

Amyda cartilaginea IRSNB 230, IRSNB 230B, IRSNB 231C, MNHNP 1883-1798, MNHNP 1883-1817, MNHNP unnumbered, NHMB 3767, PCHP 1310, RH 128, RH 129, RH 133, UF 57728, USNM 222522, ZSM 832/1920, ZSM 833/1920, ZSM 834/1920, ZSM 835/1920, ZSM 836/1920, ZSM 837/1920, ZSM 838/1920.

Aspideretes gangeticus BMNH 48.2.21.41, BMNH 80.1.28, BMNH 86.8.26.1, BMNH 3 unnumbered specimens, EOM 2663, EOM 2664, EOM 2801, MNHNP 1866-151, MNHNP A-5226, MNHNP unnumbered, SMF 52770.

Aspideretes hurum BMNH 68.2.12.15, BMNH 86.8.26.2, BMNH 81.7.8.4, BMNH 81.7.8.5, EOM 2681, EOM 2811, EOM 2826, RE 2132, ZSM 26/1912.

Aspideretes leithii BMNH 70.7.11.1, EOM 2627, EOM 2819.

Aspideretes nigricans BMNH 1929.12.23.1, BMNH 1929.12.23.2.

Chitra indica BMNH 47.3.6.21, BMNH 86.2.1.1, BMNH 87.3.30.11, BMNH 1926.12.16.1, BMNH 48.2.139, BMNH 1974.2451, BMNH 1984.1276, BMNH unnumbered (mount 220), EOM 2625, EOM 2696, EOM 2699, IRSNB 18.8.88 *(?? = 3295)*, MNHNP 1880.182, PCHP 1474, PCHP 1707, PCHP 2613, SMF 52768, SMF 52769.

Cyclanorbis elegans BMNH 64.1.25.3, BMNH 64.8.8.9, BMNH 65.5.9.22, BMNH 1900.9.22.8, BMNH 1906.11.16.2, BMNH 1909.10.15.5, BMNH 1949.1.9.58, BMNH 1954.1.14.2, BMNH 1954.1.14.3, BMNH unnumbered, NMW 157, NMW 1436, NMW 1437, NMW 1438, NMW 1439, NMW 1440, NMW 1441, NMW 1504, RMNH 17968, SMF 37475.

Cyclanorbis senegalensis BMNH 63.11.9.6, BMNH 1864.216, BMNH 65.4.6.10, BMNH 65.5.3.72, BMNH 65.5.3.73, BMNH 65.5.3.75, BMNH 65.5.9.19, BMNH 65.5.9.20, BMNH 65.5.9.21, BMNH 1920.1.20.3225, BMNH 1920.1.20.3641, BMNH 1920.1.20.4118, BMNH 1947.3.6.23, BMNH 1949.1.3.57, BMNH unnumbered, MCZ 42599, MNHNP-AC 1944-251, NMW 1257/1, NMW 1257/2, NMW 1434, SMF 37474, ZSM 2509/0.

Cycloderma aubryi BMNH 61.7.29, BMNH 63.6.13.5, FMNH 98752, MCZ 145308, MHNG unnumbered, MNHNP 1889-384, MNHNP 1922-365, MNHNP 1930-362, MNHNP 1944-265,

MNHNP-AC unnumbered, MRAC 945, MRAC 2581, MRAC 3050, MRAC 14621, MRAC 14623, MRAC 14662, MRAC 19212, MRAC 19813.

Cycloderma frenatum BMNH unnumbered (type of *Aspidochelys livingstoni*), MCZ 50359, NHMB 16692, NMZB 1245, NMZB 6623, SMF 33700, TM unnumbered, UF 52704.

Dogania subplana BMNH 53.5.38, BMNH 60.3.19.1045, BMNH 81.10.10.12, BMNH 1929.7.3.10, BMNH unnumbered, MNHNP A5182, MVZ 95937, NMW 1871, PCHP unnumbered, RMNH unnumbered, UF 56317, USNM 40005, USNM 70835, USNM 222523.

Lissemys punctata BMNH 69.8.28.10, BMNH 88.12.3.4, BMNH 1972.2067, BMNH 1972.????, MNHNP A5169, MNHNP-AC 1880-472, NHMG 615.87, NHMG 615.88, NHMG 1557.19, NMW 1872, PCHP 1437, UF 55788, UF 56017, UMMZ 129396, UMMZ 129896, USNM 061093, USNM 061094.

Nilssonia formosa BMNH 68.4.3.142, BMNH 81.7.8.3, BMNH 87.3.30.12, BMNH 87.3.30.20, BMNH 91.11.26.6.

Palea steindachneri BMNH 1930.4.3.2, MNHNP 1980/1476, MNHNP unnumbered.

Pelochelys bibroni BMNH 60.4.19.1444, BMNH 64.9.28.5, BMNH 80.4.25.6, BMNH 87.3.30.15, BMNH 99.1.12.7, BMNH 1974.2330, BMNH unnumbered, EOM 2675, NHMB 183, NMW 1857, RMNH 21839, RMNH unnumbered, USNM 231523.

Pelodiscus sinensis BMNH 62.2.23.9, BMNH 73.7.30.19, BMNH unnumbered, NHMB C1438, NHMB C1439, NHMB C2659, NHMB 3173, NMW 1868, RH 307, SMF 69850, UF 55259, UF 55265, UF 55266, UF 55267, UF 55270, UF 55271, UF 56116, USNM 68476, USNM 68833, ZSM 144/1908, ZSM 428/1911, ZSM 429/1911, ZSM 430/1911, ZSM 3020/0, ZSM 3041/0, ZSM 3043/0, ZSM 3044/0.

Rafetus euphraticus BMNH 50.12.1.1, BMNH 50.12.21.16, BMNH 54.5.11.17, BMNH 93.10.14.1, BMNH 1935.5.9.8, NMW 127, NMW 130, NMW 131, NMW 132, NMW 204, NMW 1446, NMW 1861, NMW 1862.

Rafetus swinhoei BMNH 73.7.30.125.

Trionyx triunguis BMNH 62.3.20.8, BMNH 65.4.6.9, BMNH 1911.7.27.1, BMNH 1954.1.14.4, IRSNB 3299, KNM ER 8123, KNM 3 unnumbered specimens, MNHNP A5186, MNHNP A5242, MRAC 5446, MRAC 11978, MRAC 12324, MRAC 12329, MRAC 14479, MRAC 15408, MRAC 15651, MRAC 16560, NMW 203, USNM 231704.

LITERATURE CITED

Adams, E. N.
1972. Consensus techniques and the comparison of taxonomic trees. *Syst. Zool., 21*: 390–397.

Albrecht, P. W.
1967. The cranial arteries and cranial arterial foramina of the turtle genera *Chrysemys, Sternotherus,* and *Trionyx*: a comparative study with analysis of possible evolutionary implications. *Tulane Stud. Zool., 14*:81–99.
1976. The cranial arteries of turtles and their evolutionary significance. *J. Morphol., 149*:159–182.

Allen, E. R.
1982. Life history notes, Testudines, *Trionyx ferox* (Florida softshell). Size. *Herp. Rev., 13*:49.

Anderson, J.
1875. Description of some new Asiatic mammals and chelonia. *Ann. Mag. Nat. Hist., ser. 4, 16*:282–285.

Annandale, N.
1912. The Indian mud-turtles (Trionychidae). *Rec. Indian Mus., 7*:151–179.

Barghusen, H. R., and T. S. Parsons
1966. Variation in the skull of Trionyx. *Am. Zool., 6*:566.

Baur, G.
1890. On the classification of the Testudinata. *Am. Nat., 24*:530–536.
1891a. The pelvis of the Testudinata, with notes on the evolution of the pelvis in general. *J. Morphol., 4*:345–359.
1891b. On the relations of *Carettochelys,* Ramsay. *Am. Nat., 25*:631–639.
1893. Notes on the classification and taxonomy of the Testudinata. *Proc. Am. Phil. Soc., 31*:210–225.

Bell, T.
1828. Characters of the order, families and genera of the Testudinata. *Zool. J., 3*: 513–516.

Bergounioux, P. M.
1932. Sur la place de *Trionyx* dans la classification des Cheloniens. *C. R. Seances Acad. Sci., 195*:1407–1409.
1955. Testudinata. *In* J. Piveteau (ed.), *Traite de Paleontologie,* vol. 5, pp. 486–544. Paris: Masson et Cie.

Bickham, J. W., J. J. Bull, and J. M. Legler
1983. Karyotypes and evolutionary relationships of trionychid turtles. *Cytologia, 48*: 177–183.
Bickham, J. W., and J. L. Carr
1983. Taxonomy and phylogeny of the higher categories of cryptodiran turtles based on a cladistic analysis of chromosomal data. *Copeia, 1983*:918–932.
Boddaert, P.
1770. *Over de Kraakbenige Schildpad de Testudine Cartilaginea.* Amsterdam: Kornelis van Tongerlo, 39 pp.
Boulenger, G. A.
1889. *Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History),* new ed. London: Brit. Mus. Nat. Hist., 311 pp.
Bramble, D. M., and J. L. Carr
MS. *Homology, mechanics and evolution of the trionychid plastron.*
Carpenter, K.
1981. Preneural in the evolution of *Trionyx. Copeia, 1981*:456–457.
Cartmill, M.
1978. The orbital mosaic in prosimians and the use of variable traits in systematics. *Folia Primatol., 30*:89–114.
Coldiron, R. W.
1974. Possible functions of ornament in labyrinthodont amphibians. *Occas. Pap. Mus. Nat. Hist. Univ. Kansas, 33*:1–19.
Crumly, C. R.
1982. A cladistic analysis of *Geochelone* using cranial osteology. *J. Herp., 16*:215–234.
1985. A hypothesis for the relationship of land tortoise genera (Family Testudinidae). *Studias Geologica Salamanticensia, volumen especial, 1*:115–124.
Cuvier, G.
1825. *Recherches sur les Ossements Fossiles,* 3rd ed., vol. 5, part 2. Paris: Dufour and D'Ocagne, 547 pp.
Dalrymple, G. H.
1977. Intraspecific variation in the cranial feeding mechanism of turtles of the genus *Trionyx* (Reptilia, Testudines, Trionychidae). *J. Herp., 11*:255–285.
1979. Packaging problems of head retraction in trionychid turtles. *Copeia, 1979*:655–660.
Daudin, F. M.
1802. *Histoire naturelle, générale et particulière, des Reptiles.* Paris, *2*:1–432.
De Broin, F.
1977. Contribution a l'etude des cheloniens, cheloniens continentaux de Cretace et du Tertiaire de France. *Mus. Natl. Hist. Nat., Memoires ser. C, 38*:1–366.
Deraniyagala, P.
1939. The tetrapod reptiles of Ceylon. Vol. 1. Testudinates and Crocodilians. *Ceylon J. Sci.,* 400 pp.
Dollo, M. L.
1884. Premiere note sur les cheloniens de Bernissart. *Bull. Mus. Roy. Hist. Nat. Belg., 3*:63–79.
Donoghue, M. J., and P. D. Cantino
1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. *Syst. Bot., 9*:192–202.
Dowling, H. G., and W. E. Duellman
1974. Systematic herpetology. *HISS Publ., Publ. Herpetol., 7*:302 pp.
Drewes, R. C.
1984. A phylogenetic analysis of the Hyperoliidae (Anura): Treefrogs of Africa, Madagascar, and the Seychelles Islands. *Occas. Pap. Calif. Acad. Sci., 139*:1–70.
Dumeril, A. M. C.
1856. Note sur les Reptiles du Gabon. *Rev. Mag. Zool., Paris, 8*:369–377.
Dumeril, A. M. C., and G. Bibron
1835. *Erpétologie général ou histoire naturelle complète des reptiles,* vol. 2. Paris: Roret, 682 pp.
Eiselt, V. J.
1976. Ergebnisse zoologischer Sammelreisen in der Türkei Bemerkenswerte Funde von Reptilien, II. *Ann. Naturhistor. Mus. Wien, 80*:803–814.
Fitzinger, L. J. F. J. de
1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften. Vienna, 66 pp.
1835. Entwurf einer systematischen Anordnung der Schildkröten nach den Grundsätzen der natürlichen Methode. *Ann. Wiener Mus., 1*:103–128.
Forskäl, O.
1775. *Descriptiones Animalium. Avium, amphibiorum, piscium, insectorum, vermium. Quae in itinere oriental observavit.* Hauniae 1775, Mölleri.
Frair, W.
1964. Turtle family relationships as determined by serological tests. *In* C. A. Leone (ed.), *Taxonomic biochemistry and serology,* pp. 535–544. New York: Ronald Press.
1983. Serological survey of softshells with other turtles. *J. Herp., 17*:75–79.
Gaffney, E. S.
1972. The systematics of the North American family Baenidae (Reptilia, Cryptodira). *Bull. Am. Mus. Nat. Hist., 147*:241–320.
1975. A phylogeny and classification of the

higher categories of turtles. *Bull. Am. Mus. Nat. Hist., 155*:389–436.

1976. Cranial morphology of the European Jurassic turtles *Portlandemys* and *Plesiochelys. Bull. Am. Mus. Nat. Hist., 157*: 489–543.

1977. The side-necked turtle family Chelidae: a theory of relationships using shared derived characters. *Am. Mus. Novitates, 2620*:1–28.

1979a. An introduction to the logic of phylogeny reconstruction. *In* J. Cracraft and N. Eldredge (eds.), *Phylogenetic analysis and paleontology*, pp. 70–112. New York: Columbia Univ. Press.

1979b. Comparative cranial morphology of Recent and fossil turtles. *Bull. Am. Mus. Nat. Hist., 164*:67–376.

1979c. Description of a large trionychid turtle shell from the Eocene Bridger Formation of Wyoming. *Contr. Geol., Univ. Wyoming, 17*:53–57.

1983. The cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island, Australia. *Bull. Am. Mus. Nat. Hist., 175*:361–480.

1984. Historical analysis of theories of chelonian relationship. *Syst. Zool., 33*:283–301.

Gaffney, E. S., and L. J. Meeker

1983. Skull morphology of the oldest turtles: a preliminary description of *Proganochelys quenstedti. J. Vert. Paleont., 3*: 25–28.

Geoffroy St. Hilaire, E. F.

1809. Sur les tortues molles, nouveau genre sous le nom de *Trionyx* et sur la formation des carapaces. *Ann. Mus. Natl. Hist. Nat., Paris, 14*:1–20.

Goin, C. J., and O. B. Goin

1962. *Introduction to herpetology*, 1st ed. San Francisco: W. H. Freeman, 341 pp.

1971. *Introduction to herpetology*, 2nd ed. San Francisco: W. H. Freeman, 353 pp.

Gray, J. E.

1831. *Synopsis Reptilium; or short descriptions of the species of reptiles. Part I. Cataphracta. Tortoises, crocodiles, and enaliosaurians.* London: Treütel, Würtz and Co., 78 pp.

Gray, J. E.

1844. *Catalogue of the tortoises, crocodiles, and amphisbaenians, in the collection of the British Museum.* London: Taylor and Francis, 80 pp.

1854. Descriptions of a new genus and some new species of tortoises. *Proc. Zool. Soc. London, 1852*:133–135.

1855. *Catalogue of shield reptiles in the collection of the British Museum. Part I. Testudinata (tortoises).* London: British Museum, 82 pp.

1864. Revision of the species of Trionychidae found in Asia and Africa, with the descriptions of some new species. *Proc. Zool. Soc. London, 1864*:76–98.

1869. Notes on the families and genera of tortoises (Testudinata), and on the characters afforded by the study of their skulls. *Proc. Zool. Soc. London, 1869*: 165–225.

1870. *Supplement to the catalogue of shield reptiles in the collection of the British Museum. Part I. Testudinata.* London, 120 pp.

1872. Notes on the mud-tortoises of India. *Ann. Mag. Nat. Hist., ser. 4, 10*:334.

1873a. Notes on mud-tortoises (*Trionyx*, Geoffroy), and on the skulls of the different kinds. *Proc. Zool. Soc. London, 1873*: 38–73.

1873b. Notes on Chinese mud-tortoises (Trionychidae), with the description of a new species sent to the British Museum by Mr. Swinhoe, and observations on the male organ of this family. *Ann. Mag. Nat. Hist. London, 4*:156–161.

Hasan, S. I.

1941. The shell and the mechanism of its closure in the Indian pond terrapin, *Lissemys punctata punctata* (Bonnaterre). *Proc. Indian Acad. Sci., 14*:235–249.

Hay, O. P.

1904. On the existing genera of the Trionychidae. *Proc. Am. Phil. Soc., 42*:268–274.

1908. The fossil turtles of North America. *Publ. Carnegie Inst. Washington, 75*:1–555.

Hecht, M. K., and A. L. Edwards

1977. The methodology of phylogenetic inference above the species level. *In* M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), *Major patterns in vertebrate evolution*, pp. 3–51. *NATO Advanced Study Institutes Ser.* New York: Plenum Press.

Heude, P. M.

1880. Memoire sur les Trionyx. *Memoires concernant l'histoire naturelle de l Empire Chinois par des Peres de la Compagnie de Jesus, 1*:1–38.

Hirayama, R.

1985. Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoi-

dea); a preliminary result. *Studias Geologicas Salamanticensia, volumen especial, 1*:141–158.

Huene, F. V.
1956. *Paläontologie und Phylogenie der niederen Tetrapoden.* Jena: Fischer Verlag, 716 pp.

Hummel, K.
1929. Die fossilen Weichschildkröten (Trionychia). Eine morphologisch-systematische und stammesgeschichtliche Studie. *Geol. Palaeont. Abh., 16*:359–487.

Hutchison, J. H.
1982. Turtle, crocodilian and champsosaur diversity changes in the Cenozoic of the North-Central region of western United States. *Palaeogeogr. Palaeoclimatol. Palaeoecol., 37*:149–164.

Hutchison, J. H., and D. M. Bramble
1981. Homology of the plastral scales of the Kinosternidae and related turtles. *Herpetologica, 37*:73–85.

King, M.
1985. Chromosome markers and their use in phylogeny and systematics. *In* G. Grigg, R. Shine, and H. Ehmann (eds.), *Biology of Australasian frogs and reptiles,* pp. 165–175. Sydney: Roy. Zool. Soc. New South Wales.

Kluge, A. G., and J. S. Farris
1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool., 18*:1–32.

Lacépède, B. G. E. de
1788. *Histoire naturelle des quadrupèdes et des serpents.* Paris: vol. 1, pp. 1–651.

Lauder, G. V.
1982. Historical biology and the problem of design. *J. Theor. Biol., 97*:57–67.

LeSueur, C. A.
1827. Note sur deux especes de tortues, du genre *Trionyx* de Geoffroy St. Hilaire. *Mem. Mus. Natl. Hist. Nat. Paris, 15*: 257–268.

Loveridge, A.
1942. Scientific results of a fourth expedition to forested areas in East and Central Africa, Part IV, Reptiles. *Bull. Mus. Comp. Zool., 91*:237–373.

Loveridge, A., and E. E. Williams
1957. Revision of the African tortoises and turtles of the suborder Cryptodira. *Bull. Mus. Comp. Zool., 115*:163–557.

Lydekker, R.
1889. *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History), Part III (Containing the order Chelonia).* London: Taylor and Francis, 239 pp.

Maddison, W. P., J. J. Donoghue, and D. R. Maddison
1984. Outgroup analysis and parsimony. *Syst. Zool., 33*:83–110.

Marx, H., and G. B. Rabb
1972. Phyletic analysis of fifty characters of advanced snakes. *Fieldiana (Zool.), 63*: 1–321.

Maslin, T. P.
1952. Morphological criteria of phyletic relationships. *Syst. Zool., 1*:49–70.

McDowell, S. B.
1961. On the major arterial canals in the ear-region of testudinoid turtles and the classification of the Testudinoidea. *Bull. Mus. Comp. Zool., 125*:23–39.

McNab, B. K.
1978. The evolution of endothermy in the phylogeny of mammals. *Am. Nat., 112*: 1–21.

Meylan, P. A.
1985. Evolutionary relationships of Recent trionychid turtles: evidence from shell morphology. *Studias Geologica Salamanticensia, volumen especial, 1*:169–188.

Meylan, P. A., and W. Auffenberg
1986. New land tortoises (Testudines: Testudinidae) from the Miocene of Africa. *Zool. J. Linn. Soc., 86*:279–307.

Meylan, P. A., and R. G. Webb
1988. *Trionyx swinhoei* (Gray) 1873, a valid species of living soft-shelled turtle (Family Trionychidae) from China. *J. Herp., 22.*

Mlynarski, M.
1976. Testudines. *In* O. Kuhn (ed.), *Handbuch der Palaoherpetologie,* part 7, pp. 1–130. Stuttgart: Gustav Fischer Verlag.

Nelson, G.
1979. Cladistic analysis and synthesis: principles and definitions, with a historical note on Adanson's Familles des Plantes (1763–1764). *Syst. Zool., 28*:1–21.

Ogushi, K.
1911. Anatomische Studien an der japanischen dreikralligen Lippenschildkröte (*Trionyx japanicus*). *Morphol. Jahrb., 43*: 1–106.

Owen, R.
1853. *Descriptive catalogue of the osteological series contained in the museum of the Royal College of Surgeons of England. Vol. 1. Pisces, reptilia, aves, marsupi-*

alia. London: Taylor and Francis, 350 pp.

Parsons, T. S., and E. E. Williams
1961. Two Jurassic turtle skulls: a morphological study. *Bull. Mus. Comp. Zool., 125*:43–107.

Peters, W. K. H.
1854. Ubersicht der auf seiner Reise nach Mossambique beobachteten Schildkröten. *Monatsber. Akad. Wiss. Berlin, 1854*:215–216.

Porter, K. R.
1972. *Herpetology.* Philadelphia: W. B. Saunders, 524 pp.

Pritchard, P. C. H.
1967. *Living turtles of the world.* Jersey City, N.J.: T. F. H. Publications, 288 pp.
1979a. Taxonomy, evolution and zoogeography. *In* M. Harless and H. Morlock (eds.), *Turtles: perspectives and research,* pp. 1–42. New York: Wiley.
1979b. *Encyclopedia of turtles.* Neptune, N.J.: T. F. H. Publications, 895 pp.
1984. Piscivory in turtles, and evolution of the long-necked Chelidae. *Symp. Zool. Soc. London, 52*: 87–110.

Rafinesque, C. S.
1832. Description of two new genera of soft shell turtles of North America. *Atlantic J. Fr. Knowl., 1*:64–65.

Ramsay, E. P.
1886. On a new genus and species of fresh water tortoise from the Fly River, New Guinea. *Proc. Linn. Soc. New South Wales, ser. 2, 1*:158–162.

Richmond, N. D.
1964. The mechanical functions of the testudinate plastron. *Am. Midl. Nat., 72*:50–56.

Romer, A. S.
1956. *Osteology of the reptiles.* Chicago: Univ. of Chicago Press, 772 pp.
1966. *Vertebrate paleontology,* 3rd ed. Chicago: Univ. of Chicago Press, 468 pp.

Schneider, J. G.
1783. *Allgemeine Naturgeschichte der Schildkröten, nebst einem system. Verzeichnisse der einzelnen Arten.* Leipzig, 364 pp.

Schumacher, G. H.
1973. The head muscles and hyolaryngeal skeleton of turtles and crocodilians. *In* C. Gans and T. S. Parsons (eds.), *Biology of the Reptilia,* vol. 4, pp. 101–199. New York: Academic Press.

Siebenrock, F.
1897. Das Kopfskelet der Schildkröten. *Sitzungsb. Akad. Wissensch., Wien. Math. Natur. Kl., 106*:245–328.
1902. Zur Systematik der Schildkrötenfamilie Trionychidae Bell, nebst der Beschreibung einer neuen Cyclanorbis-Art. *Sitzungsb. Akad. Wissensch., Wien, 111*: 807–846.
1906. Zur kenntnis der schildkrötenfauna der Insel Hainan. *Zool. Anz., 30*:578–586.
1909. Synopsis der rezenten Schildkröten, mit Berücksichtigung der in historischer Zeit ausgestorbenen Arten. *Zool. Jahrb., Suppl., 10*:427–618.
1913. Schildkröten aus Syrien und Mesopotamien. *Ann. Nat. Hofmus. Wien, 27*: 171–225.

Smith, H. M., and L. F. James
1958. The taxonomic significance of cloacal bursae in turtles. *Trans. Kansas Acad. Sci., 61*:86–96.

Smith, H. M., and R. B. Smith
1980. *Synopsis of the herpetofauna of Mexico. Vol. VI. Guide to Mexican Turtles.* North Bennington, Vt.: John Johnson, 1044 pp.

Smith, M. A.
1931. *The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Vol. 1. Loricata, Testudines.* London: Taylor and Francis, 185 pp.

Stearns, S. C.
1984. The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. *Am. Nat., 123*:56–72.

Stejneger, L.
1944. Notes on the American soft-shell turtles with special reference to *Amyda agassizii. Bull. Mus. Comp. Zool., 94*:1–75.

Strauch, A.
1890. Bemerkungen über die Schildkrötensammlung im zoologischen Museum der Kaiserlichen Akademie der Wissenschaften zu St. Petersburg. *Mem. Acad. Sci. St. Petersburg, ser. 7, 38*:1–127.

Suzuki, H. K.
1963. Studies on the osseous system of the slider turtle. *Ann. N.Y. Acad. Sci., 109*: 351–410.

Swofford, D. L.
1984. *PAUP. Phylogenetic analysis using parsimony. Version 2.3.* Unpub. documentation. Champaign, Illinois.

Vaillant, L.
1876. Remarque sur la disposition des vertebres cervicales chez les Trionyx. *Bull. Soc. Philomatique de Paris, ser. 7*:239.

Villiers, A.
1958. Tortues et crocodiles de l'Afrique Noire francaise. *Initiations Africaines, 15*:1–354.
Waite, E.
1905. Osteology of the New Guinea turtle. *Rec. Austral. Mus., 6*:110–118.
Walker, W. F.
1973. The locomotor apparatus of Testudines. *In* C. Gans and T. S. Parsons (eds.), *Biology of the Reptilia. Vol. 4. Morphology,* pp. 1–100. London, New York: Academic Press.
Walther, W. G.
1922. The New-Guinea turtle *Carettochelys insculpta* Ramsay. *Nova-Guinea, 13*: 607–704.
Watrous, L. E., and Q. D. Wheeler
1981. The out-group method of character analysis. *Syst. Zool., 30*:1–11.
Webb, R. G.
1962. North American Recent soft-shelled turtles (Family Trionychidae). *Univ. Kansas Publ. Nat. Hist., 13*:429–611.
1982. Taxonomic notes concerning the trionychid turtle *Lissemys punctata* (Lacepede). *Amphibia-Reptilia, 3*:179–184.
Wermuth, H., and R. Mertens
1961. *Schildkröten-Krokodile-Brückenechsen.* Jena: Gustav Fischer Verlag, 422 pp.
Wiegmann, A. F. A.
1835. Beiträge zur Zoologie, gesammelt auf einer Reise um die Erde, von Dr. F. J. F. Meyen. Siebente Abhandlung. Amphibien. *Nova Acta Phys. Med. Acad. Caesar. Leop.-carol, 17*:183–268d.
Wheeler, Q. D.
1986. Character weighting and cladistic analysis. *Syst. Zool., 35*:102–109.
Wiley, E. O.
1981. *Phylogenetics, the theory and practice of phylogenetic systematics.* New York: Wiley, 439 pp.
Williams, E. E.
1950. Variation and selection in the cervical central articulations of living turtles. *Bull. Am. Mus. Nat. Hist., 94*:509–561.
1952. A staurotypine skull from the Oligocene of South Dakota. *Breviora, 2*:1–16.
Williams, E. E., and S. B. McDowell
1952. The plastron of soft-shelled turtles (Testudinata, Trionychidae): a new interpretation. *J. Morphol., 90*:263–280.
Wirot, N.
1979. *The turtles of Thailand.* Bangkok: Mitbhadung Press.
Young, C. C., and M. C. Chow
1953. New fossil reptiles from Szechuan China. *Acta Scientica Sinica, 2*:216–243.
Zangerl, R.
1939. The homology of the shell elements in turtles. *J. Morphol., 65*:383–406.
1959. Rudimentare Carapaxbeschuppung bei jungen Exemplaren von *Carettochelys* und ihre morphogenetische Bedeutung. Naturforsch. *Gesellschaft Zürich, Jahrg. 104*:138–147.
1969. The turtle shell. *In* C. Gans (ed.), *Biology of the Reptilia,* vol. 1, pp. 311–339. New York: Academic Press.
Zangerl, R., and W. D. Turnbull
1955. *Procolpochelys grandaeva* (Leidy), an early carettine sea turtle. *Fieldiana (Zool.), 37*:345–382.
Zug, G. R.
1966. The penial morphology and the relationships of cryptodiran turtles. *Occas. Pap. Mus. Zool. Univ. Michigan, 647*: 1–23.
1971. Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles. *Mus. Zool. Univ. Michigan. Misc. Publ., 142*: 1–98.